QK1
.L5642
1913-22
v.8

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY

OF

LONDON.

SECOND SERIES.—VOLUME VIII.

BOTANY.

B19.70

LONDON:

PRINTED BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON HOUSE, PICCADILLY, W. 1;

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER ROW, E.C. 4.

1913–1922.

MISSOURI BOTANICAL
RECEIVED
APR 18 1927
GARDEN LIBRARY.

CONTENTS.

PART I.—January, 1913.

I. *A Contribution to a Knowledge of the Mutating Œnotheras.* *By* Reginald R. Gates, *M.A., Ph.D., Royal College of Science, South Kensington.* (*Communicated by* Prof. J. Bretland Farmer, *F.R.S., F.L.S.*) (Plates 1–6.) pages 1–68

PART II.—May, 1913.

II. 1.—*On some Indian Jurassic Gymnosperms* (Plates 7–9), *and* 2.—Rhexoxylon africanum, *a new Medullosean Stem* (Plates 10 & 11). *By* Nellie Bancroft, *B.Sc.* (*Lond.*), *F.L.S.*, 1851 *Research Scholar, Newnham College, Cambridge.* 69–103

PART III.—October, 1913.

III. *Marine Algæ*, Rhodophyceæ, *of the 'Sealark' Expedition, collected by Mr. J. Stanley Gardiner, M.A.* *By* Mrs. A. Weber-Van Bosse, *Ph.D.* (*Communicated by* Prof. J. Stanley Gardiner, *M.A., F.R.S., F.L.S.*) (Plates 12–14 and 1 Text-figure.) 105–142

PART IV.—December, 1913.

IV. *Observations on the Morphology and Anatomy of the Genus* Mystropetalon, *Harv.* *By* R. J. Harvey Gibson, *M.A., F.L.S., Professor of Botany in the University of Liverpool.* (Plates 15 & 16.) 143–154

PART V.—December, 1913.

V. *On the Cuticles of some Recent and Fossil Cycadean Fronds.* *By* H. Hamshaw Thomas, *M.A., F.G.S., Curator of the Botanical Museum, Cambridge, and* Nellie Bancroft, *B.Sc., F.L.S.*, 1851 *Research Scholar, Newnham College, Cambridge.* (Plates 17–20 and 32 Text-figures.) 155–204

PART VI.—July, 1914.

VI. *An Anatomical Study of the Palæozoic Cone-genus* Lepidostrobus. *By* Agnes Arber, *D.Sc., F.L.S., Fellow of Newnham College, Cambridge.* (Plates 21–27 and 4 Text-figures.) 205–238

PART VII.—December, 1914.

VII. *A Contribution to the Study of the Evolution of the Flower, with special reference to the* Hamamelidaceæ, Caprifoliaceæ, *and* Cornaceæ. *By* Arthur Samuel Horne, *B.Sc., F.L.S., F.G.S., Lecturer on Botany in the Royal Horticultural Society's School of Horticulture.* (Plates 28–30 and 13 Text-figures.) . 239–309

PART VIII.—December, 1915.

VIII. *Notes on the Morphology of certain Structures concerned in Reproduction in the Genus* Gnetum. *By* H. H. W. Pearson, *Sc.D., F.L.S., Henry Bolus Professor of Botany in the South African College.* (Plates 31 & 32.) . . . 311–332

On Isoëtes japonica, *A. Br.* *By* Cyril West, *F.L.S., and* H. Takeda, *D.I.C.* (Plates 33–40 and 20 Text-figures.) 333–376

PART IX.—September, 1922.

Titlepage, Contents, and Index 377–386

2nd Ser. BOTANY.] [VOL. VIII. PART 1.

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

A CONTRIBUTION TO A KNOWLEDGE OF THE MUTATING OENOTHERAS.

BY

REGINALD R. GATES, M.A., Ph.D., Royal College of Science, South Kensington.

(*Communicated by* Prof. J. BRETLAND FARMER, F.R.S., F.L.S.)

[PLATES 1–6.]

LONDON:

PRINTED FOR THE LINNEAN SOCIETY

BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON-HOUSE, PICCADILLY, W.

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

January 1913.

TRANSACTIONS

OF

THE LINNEAN SOCIETY.

I. *A Contribution to a Knowledge of the Mutating Oenotheras.* *By* REGINALD R. GATES, *M.A., Ph.D.; Royal College of Science, South Kensington.* (*Communicated by* Prof. J. BRETLAND FARMER, *F.R.S., F.L.S.*)

(Plates 1–6.)

Read 7th November, 1912.

CONTENTS.

	Page
I. Introduction	1
II. Conspectus of Species and Mutations of the *Onagra* group of *Oenothera*	11
Key to *Oenothera* species of the *Onagra* group	12
III. Relationships of Species	14
IV. Variations and Mutations of *O. Lamarckiana*, Ser.	20
O. grandiflora, Solander	38
O. biennis, Linn.	39
O. muricata, Linn.	40
V. (A) Cultures of Oenotheras from Lancashire	43
(B) Cultures from Botanical Gardens	47
VI. Hybridization in *Oenothera*	48
(*a*) Crosses involving *O. Lamarckiana* and its Mutants	48
(*b*) „ with *O. gigas*	50
(*c*) „ between *O. biennis* and *O. Lamarckiana* and its derivatives	52
(*d*) Results	55
VII. General Considerations and Summary	58
VIII. Bibliography	62
IX. Explanation of the Plates	64

I. INTRODUCTION.

THE purpose of the present paper is to bring together and organize certain results of experimental work which I have carried on with the Oenotheras during the last six years. My cytological work with these forms, which is already well known, will only

be referred to incidentally, the main purpose being the presentation of certain results of studies in variation and hybridization with these forms, and a discussion of their general bearing on our view-point with regard to the mutation problem in *Oenothera*.

I may say at the outset that my purpose has been to study these mutation phenomena from as many points of view as possible, in the belief that all the data from every source could finally be brought together and applied in the explanation of the evolutionary significance of this type of behaviour. The greater the amount of information already at hand with regard to any group of forms, the wider is the basis of interpretation for all additional facts, and I have therefore felt that more could be gained by attempting to consider a single group of organisms from every angle than by studying forms belonging to many genera from any given point of view—*e. g.*, that of cytology or hybridization. This is my apology for continuing to devote my attention to one somewhat limited group. I believe this intensive method is a valuable one, and in the present state of our knowledge is to be recommended for other genera as well.

I have therefore studied the Oenotheras, not only as regards their cytology, but in the details of their external characters, their variability, and hereditary behaviour. This has involved also a study of the history of the mutating and related species in cultivation, and as naturalized in Europe and other parts of the world; as well as numerous cultures of wild forms from many parts of the North American continent, to determine the relationships and distribution of the many geographic races. The results are of course very incomplete, and even fragmentary, but I think the method is amply justified by certain results already obtained: for example, the way in which the cytological structure of *O. gigas* and its peculiar behaviour in crossing are of mutual help in explaining each other; and the manner in which cultures of certain wild forms of *O. muricata* from Canada have thrown light on the probable origin and significance of the twin types in certain hybrids of *O. Lamarckiana*.

The large quantity of data with regard to the mutating Oenotheras which has accumulated since the publication of 'Die Mutationstheorie' by DeVries (1901–3) has led to a number of modifications of the views expressed by the author of that monumental work with reference to the mutation phenomena which he first described.

Subsequent studies of *Oenothera Lamarckiana* by MacDougal (1903, 1905, 1907), myself, and others have confirmed in a general way the accuracy of DeVries's observations concerning the hereditary behaviour of this species. The general facts regarding the sudden, occasional, discontinuous origin of aberrant types which breed true have been amply confirmed. But there remains the all-important question of the evolutionary significance of this and similar behaviour. For an adequate interpretation of these phenomena, much fuller data in a variety of directions were required. Some of these data have now been supplied, and have thrown new light on the nature and meaning of the process.

A more detailed discussion of the mutation phenomena in *Oenothera Lamarckiana* will be taken up in later sections of this paper. In this introductory statement it will be well to view the mutation theory in certain of its broader aspects, and to ask what

place can now be assigned to mutation as an evolutionary factor. Without anticipating the more minute analysis of the mutation process in *Oenothera*, I may be permitted to state certain points of view at which I have arrived.

One of the facts which I shall be particular to emphasize in this paper is that, although a continuous series can be formed between a mutant and its parent in the case of many characters, yet each of the mutants is actually discontinuous in its origin, its organs exhibiting a decided break from those of the parent.

If a colony of *O. Lamarckiana* and its mutants were growing together in large numbers, any casual observer would probably consider that they represented one general widely-variable or polymorphic species. Yet experiments show that each type originates discontinuously, and that the differences, which are exhibited in every organ, are as great as are to be seen in elementary species. Some of the forms would very probably be given specific rank by "splitters" if they were collected wild, while the others would certainly rank at least as varieties, or forms.

It has to be remembered, however, that in cultures the characters are better displayed and developed than can usually be the case with wild forms under conditions of competition with surrounding vegetation. In this sense, and also through improvement in the conditions of nutrition, cultivation brings out differences which would otherwise escape the observer, but it is probable that there is no other direct effect of cultivation, at least in early years. There is, however, some rather cogent evidence (*cf.* Hill, 1912) for the view commonly held by horticulturists, that after a period of years, cultivation induces variability. Darwin also believed in the existence of this effect, which he ascribed to "changed conditions." Definite experimental proof of such an effect is greatly needed. It seems probable that change of climate or of soil might account for all such cases of induced variability, rather than any direct effect (such as increased nutrition or freedom from competition) of cultivation itself. Many such cases are, of course, to be explained by crossing.

This brings us to a consideration of the status of *O. Lamarckiana*. As regards its characters, it is undoubtedly a "good species," differing throughout from *O. grandiflora*, *O. biennis*, and *O. muricata*, its nearest relatives. Its mutants are grouped like a constellation of satellites around it, and none of them exhibit any character closely approaching any other known species. Nearly all agree with *O. Lamarckiana* in certain bud-characters and in pubescence, though they all differ markedly in foliage. As regards the cause of this type of "variability," several reasons might be ascribed: (1) crossing; (2) change of climate or other effect of cultivation; (3) internal mutational changes independent of any of these.

Considering the first of these, it is clear that *O. Lamarckiana*, like all other open-pollinated plants, must have at one time undergone crossing. This fact has been emphasized in another paper (Gates, 1911 *d*), and here I need only state that whether *O. Lamarckiana* originally existed in the wild state as an isolated species or, as seems more probable, was only one of many freely intercrossing races along with certain forms of *O. grandiflora*, is immaterial if we admit, as we must, that open-pollinated colonies

of plants freely intercross. This is the condition under which their evolution takes place. If, as some think, *O. Lamarckiana* originated in Gardens through crossing between, e. g., *O. grandiflora* and *O. biennis*, then it would probably have also originated long previously through crossing where these occupied the same area in Eastern North America. Indeed, this conclusion is difficult to avoid, and I have previously shown (Gates, 1911 *a*) that both *O. biennis* and *O. grandiflora* survived in the region of Virginia and Carolina until a century ago.

As discussed later in this paper, a Lancashire colony of Oenotheras which has existed for certainly over a century, contains *O. Lamarckiana* as the dominant form. Such facts as these serve to show that the essential points to decide in determining the status of mutation as an evolutionary factor are, (1) will *O. Lamarckiana* survive in competition with its near relatives, and (2) will the mutants survive in competition with *O. Lamarckiana*. The former point has already been settled affirmatively by a study of the Lancashire colony already mentioned. The only actual evidence yet obtained for the latter is the fact that DeVries found certain forms, such as the putative mutants *O. brevistylis* and *O. laevifolia*, persisting year after year with *O. Lamarckiana*, in the field at Hilversum near Amsterdam where they were originally found. Competition experiments will be required before it can be known which of the mutants will survive under various climatic conditions.

DeVries has emphasized the fact that certain of the mutants seem to differ in their physiological adjustments or adaptations; *O. gigas*, for instance, being more strongly biennial than the other forms. But the value of any such differences can only be determined by actual experiments on the survival of the mutants under various climatic conditions.

The ingenious theory of DeVries, that new forms appear suddenly, already adapted to various environments, and are afterwards so distributed that each reaches the environment for which it is most fitted, in spite of certain obvious difficulties regarding its survival during the period of its distribution, may account for certain cases of what we may call climatic adaptation. But such a principle can scarcely be extended to the more complex cases of adaptation in plants and animals which it is one of the main duties of evolutionists to explain. I may quote the celebrated passage from Darwin ('Origin of Species,' 6th Edition, page 2) in which he cites two such cases:—"It is preposterous to attribute to mere external conditions, the structure, for instance, of the woodpecker, with its feet, tail, beak, and tongue, so admirably adapted to catch insects under the bark of trees. In the case of the mistletoe, which draws its nourishment from certain trees, which has seeds which must be transported by certain birds, and which has flowers with separate sexes absolutely requiring the agency of certain insects to bring pollen from one flower to the other, it is equally preposterous to account for the structure of this parasite, with its relations to several distinct organic beings, by the effects of external conditions, or of habit, or of the volition of the plant itself."

It seems almost equally incredible that a series of chance mutations could account for

the origin of such complex biological relationships. Darwin's principle of natural selection, although unproven in such cases, still remains the only adequate theoretical explanation.

To return to the question of crossing, and its effect upon *O. Lamarckiana* in relation to the mutation phenomena: as I have stated elsewhere, it seems probable that this behaviour is an expression of the germinal instability resulting from crossing of races in the ancestry of the parent form. It is evidently not the re-appearance of forms which entered into that ancestry, nor is it merely a case of hybrid splitting as that is now understood. DeVries has classified mutations as progressive, retrogressive, and degressive, the last being the re-appearance of characters which had previously disappeared. From my study of the mutants of *Oenothera* they appear to me to be (1) positive, due to plus variation in one or more characters, of which *O. rubricalyx* is an example; (2) negative, due to the minus variation or loss of one or more characters, e. g., *O. nanella*; and (3) mutations involving a divergent change in various characters to a new condition of equilibrium. Most of the mutants of *Oenothera* belong to the last category, and even the positive and negative mutations involve changes in all the other organs in most cases—e. g., *O. gigas*, *O. lata*, *O. nanella*. Occasional positive or negative mutants occur in *Oenothera*, in which only one character is affected—*e. g.*, pigmentation in *O. rubricalyx*. Mutations affecting single characters appear to be much more common in other genera. But it is not certain that there is a real distinction here between qualitative and quantitative mutations. In any case, DeVries is doubtless correct that whether a single character or many are affected, the originating cause in each case is a single germinal change. Changes which affect every organ, including foliage and flower characters, are probably more fundamental than those affecting only colour characters, or the size of a particular organ.

I have elsewhere pointed out (Gates, 1911 *d*, p. 599) that the appearance of the mutants *O. gigas* and *O. rubricalyx* cannot be accounted for on the basis of hybrid splitting, and also that the mutational changes may occur at different points in the life cycle. The evidence for the heterozygous character of the original *O. rubricalyx* mutant, and hence for the occurrence of this particular change during the reduction divisions in one spore mother-cell, is particularly clear; while the evidence from the tetraploid number of chromosomes in *O. gigas* (Gates, 1911 *c*) makes it probable that the change here may have occurred in the fertilized egg or in an apogamously developed megaspore *. The theory of DeVries regarding the origin of the mutants has been that in every case the change occurred in the spore mother-cells, each mutant originating from the union of the product of a mutated and a non-mutated spore. There are, however, obvious difficulties with this view, as will be pointed out in a moment. My cytological work (see Gates, 1908) with the Oenotheras showed the presence of

* Since this was written, Stomps (1912) and Miss Lutz (1912) have observed triploid mutants from *Lamarckiana* having 21 chromosomes. This increases the probability that tetraploid mutants may originate from the union of two unreduced germ-cells, but it by no means shows that they do not also originate in the manner I have suggested. I shall discuss this matter in detail elsewhere.

occasional irregularities in the distribution of chromosomes during meiosis, which furnish a possible basis for the origin of negative mutants, provided that the chromosomes in *Oenothera* are qualitatively different. But since the chromosomes of these plants are morphologically undifferentiated, there is at present no opportunity of following this possibility further. Chromosome distributions in the germ-cells are doubtless concerned in the origin of mutants having 15 or 16 chromosomes.

To return to the difficulty regarding the hypothesis that a mutation is of hybrid nature, arising from the fusion of a mutated with an unaltered cell, let us suppose, for instance, that *O. rubrinervis* arises from a mutated germ-cell crossed with an ordinary *O. Lamarckiana* germ-cell. If this is so, why does *O. rubrinervis* breed true when self-pollinated, yet when crossed with *O. Lamarckiana* it splits in the F_1 giving *O. Lamarckiana* and *O. rubrinervis*, both of which remain constant in later generations? It might be said that the primary "mutated" germ-cell was different from a *rubrinervis* germ-cell, but that when crossed with *O. Lamarckiana* it gave a combination which bred true and produced the *rubrinervis* characters. However, if this were admitted, there is no reason for supposing that our *rubrinervis* germ-cell when crossed with *O. Lamarckiana* would behave in an entirely different manner and give alternative inheritance. To explain the origin of a mutation on this basis, one must assume a change in the hereditary behaviour of the germinal material in two successive generations where one would expect it to be the same. Why should a mutated germ-cell, crossed with a non-mutated one, give a blend which never splits, while the germinal material derived from this blend, when crossed with another non-mutated germ-cell of *O. Lamarckiana*, always exhibits alternative inheritance? Such a condition of affairs is conceivable but not probable. It involves a paradox which has not yet been explained away.

Leclerc du Sablon (1910) has formulated the ingenious hypothesis that the phenomena of mutation in *O. Lamarckiana* are to be explained as a case of Mendelian splitting in which there is a very high degree of "coupling" between the characters. But this seems to be merely putting the facts into another notation without really adding to our knowledge of why the new forms appear. Moreover, it fails to take account of the change in chromosome number in *O. gigas*. This nuclear change places *O. gigas* in a different category from the other mutants.

I have already mentioned the hypothesis that the mutants may be due to occasional irregularities in the distribution of the meiotic chromosomes. Another, and possibly more probable, explanation is that though the mutations are internal in origin, yet they are released by an external stimulus which affects the cytoplasm, and indirectly the nuclear structure. If this is an approach to the true explanation, the releasing stimuli must be very slight. This view is difficult to harmonize with the fact that the mutants seem to appear with about the same frequency wherever *O. Lamarckiana* is cultivated. However, comparatively little is known concerning such environmental responses in organisms.

Finally, we may agree that mutation, in so far as it is distinguished from hybrid-splitting (see p. 47), probably accounts for much species-formation. Many polymorphic genera are probably indebted to such a process for the large number of closely

related forms they contain. It seems evident that in many cases the differences between these elementary species (using the term in DeVries's sense) are not of value for selection. The limits of natural selection as an eliminating factor are probably much more circumscribed than extreme selectionists have supposed.

If we refer briefly to other factors which are evidently concerned in species-origin and evolution, we must compare mutation, as an evolutionary factor, with natural selection. If there is any one point in Darwinian natural selection which has not been fully appreciated in post-Darwinian discussions, it is, perhaps, that Darwin assumed, at least in most cases, an original environmental change for the organism, which led to the necessity for its readjustment to its environment, modification of the species being produced during this period of readjustment. Thus the change in the climate of a given area or the introduction of a species into a new area with different environmental conditions are continually referred to by Darwin as the initial changes leading to modification of particular species. When no environmental changes were taking place, natural selection was looked upon as maintaining the nicely-balanced equilibrium between the species. It is always a climatic change, or the entrance of new organisms, which disturbs that equilibrium, and natural selection then becomes a factor producing modification. True, Darwin often emphasizes the keenness of the struggle for existence, and its effect in bringing and maintaining all the organs of the competing organisms at their highest degree of efficiency. But when some new departure is to be made in the structure of any organism, a primary environmental change is first supposed to throw the organism to one side of the centre of its equilibrium, this being followed by progressive change through the effects of the selection of variations, until the organism is once more adjusted to the mean of its organic and inorganic environment.

Two distinct effects of natural selection were therefore recognized by Darwin: (1) a conservative effect, maintaining the race at its highest degree of efficiency while the environmental conditions remain unchanged; and (2) a modificational effect, causing the selection of new variations and the final establishment of a new equilibrium when the previous equilibrium has been disturbed by an organic or an inorganic environmental change.

Darwin's distinction between these two independent effects of natural selection is by no means always clear. But recent experimental work, particularly, has emphasized the importance of natural selection as a conservative force, maintaining the condition of equilibrium which exists between any organism and its whole environment. It is a condition to which organisms have been almost universally subjected during the whole period of evolution. But it is not a force, and it is not as constant and unintermittent in its effect, as, *e. g.*, gravitation. The *modificational* effect of selection has, on the other hand, thus far remained unproven, notwithstanding the experimental researches of the last decade. As a result of the negative evidence from experimental work, we are now in much the same position with regard to both selection and the inheritance of acquired modifications. They are still unproven, though there is a certain amount of

rather incomplete and not-fully-convincing evidence for both. The Lamarckian factor, which has always received support from anatomists and palæontologists, has in recent years experienced a distinct renaissance, particularly in the attempts of Semon, Rignano, and others to eliminate its main weakness by formulating a biological mechanism by means of which the transmission of acquired modifications could take place.

To return to mutation and selection, the latter at least, and perhaps also the former, requires "changed conditions" in order to produce a modificational effect. But the vicissitudes of changing climates and distributions cannot be sufficient to produce the orderly phylogenies which frequently appear when we view larger groups of organisms as a whole, and especially when we consider the broader outlines of the palæontological record. Hence, at this point both mutation and selection appear to break down as evolutionary factors. The larger simultaneous evolutionary trends exhibited in the history of organisms appear to present problems which are more or less apart from mere questions of species-formation in each group. These problems, together with those of the origin of phyla, have been comparatively little realized in the literature of experimental evolution. On the other hand, the experimental researches of the last decade have made it more plain how closely is species-origin in each group bound up with the biological inter-relationships of the organisms composing that group. By such means it may be possible ultimately to distinguish between factors leading to the production of more or less incidental and evanescent species, and those which have been more vitally concerned in the phylogeny of the group. It seems at present that mutations such as occur in *Oenothera Lamarckiana* are chiefly incidental, rather than phylogenetic in value, though the lack of perspective in the case of such recent productions makes it difficult to judge of their real value. The only final way to answer this question is by determining whether the mutants will survive in competition and leave descendants.

Perhaps we may sum up the present status of evolutionary investigation with the statement that recent researches have resulted chiefly in revealing the inadequacy of single factors, such as natural selection and mutation, to account for all evolution. Both these factors have doubtless played their part, however, together with the neo-Lamarckian factor, orthogenesis, and other factors, some of which have doubtless not yet been perceived. New organisms do not arise by any single method, but evolution is a multifarious process, and the deeper currents of evolutionary progress are still very little understood.

The greatest advances since Darwin have been made in our experimental knowledge of heredity and its structural basis, and in the laws of variability. The foundations for the laws of inheritance laid by the experiments of Mendel, and so rapidly developed and amplified by Bateson and the Mendelian school with active workers in several countries, have shown at least one fundamental fact—namely, the alternative expression of many characters on crossing, in a wide range of plants and animals. It remains to

determine how the segregational type of behaviour is related to blended inheritance, and what features the two have in common.

As regards the laws of variability, we have been enabled to draw a sharp distinction between heritable and non-heritable variations, although, since character-changes having the same external appearance may belong in either category, we cannot safely predict what the behaviour of a variation will be in any case until it is experimentally tested. Notwithstanding the attention which has been focussed on discontinuous variations or mutations in recent years, particularly by the work of DeVries, even those which are evidently due to the simple loss of characters are still largely beyond the range of our explanation. But it may reasonably be hoped that with further knowledge of their origin and causes they may be brought, at least to a limited extent, under experimental control. Any further advances in this direction will be of great theoretical as well as practical value.

These investigations with *Oenothera* have been carried out at the University of Chicago, the Marine Biological Laboratory, Woods Hole, Mass., and the Missouri Botanical Garden. They were continued last year at the John Innes Horticultural Institution, Merton, Surrey. To the Directors of all these institutions I am very greatly indebted, for the facilities afforded for carrying on my cultures, and keeping photographic and other records. I am also indebted to the Carnegie Institution for a grant in aid of expenses in 1908. I have further to thank Professor Farmer for suggestions in connection with the preparation of this paper, and a Grant from the Royal Society has defrayed the expenses of publishing the plates. Numerous botanists from many parts of the world have very kindly sent me seeds of *Oenothera* species, and I shall be most grateful to any botanists who will send me further seeds of wild or naturalized species from any country. The study of naturalized colonies of *Oenothera* will furnish an important part of the data required.

In connection with these cultures, as the variety of races under observation has multiplied, and the number of new forms recognized has increased, the difficulties in connection with the adoption of a method of nomenclature which would be serviceable to experimental evolutionists and at the same time acceptable to systematists have become increasingly pressing. After much thought and discussion on the subject, and consultation with Dr. O. Stapf, F.R.S., Keeper Royal Herbarium, Kew, and Dr. A. B. Rendle, F.R.S., British Museum (Natural History), I venture to suggest the following usages.

The names of forms which are (1) known only in cultures, or (2) which have originated in cultivation, or (3) the description of the behaviour of which is based on material long in cultivation, shall be followed by the abbreviation *cult.*, to distinguish them from forms derived directly from wild sources.

This usage is already followed partly by systematists, and may perhaps be adopted with advantage by breeders. Like every rule, however, there will be plenty of

difficulties in its application, and judgment will be necessary in deciding each case. The greatest difficulty will probably be in connection with (3), in determining how many years of culture may elapse before a given form must be considered "in cultivation." It has always been the case, and rightly so, that many species were described by systematists from the growing plants; and the modern tendency is to describe species as far as possible from their living characters. Obviously, such forms are not to be classed as cultivated species. But when new forms are recognized and segregated after many years of culture they may perhaps fairly be considered as "cultivated" forms. The fact that such species were first recognized in cultures will not, however, justify the assumption that they do not also occur wild. Also, the use of the term, with, e. g., *O. Lamarckiana*, Ser., does not necessarily mean that the species originated in cultivation, but merely that the material under discussion was derived from a race long in cultivation. Thus, the same species may be referred to in one connection as a wild, and at another time as a cultivated form.

Similarly, mutations or forms which have originated through germinal changes under experimental control, so that the history of their origin is known, should be preceded by the abbreviation *mut.*

The greatest value of the usage suggested above, and, indeed, the reason for this suggestion, lies in the fact that it will enable breeders to use the convenient binomial terminology for forms which are in many cases not strictly comparable to wild species, without the danger of their being mistaken for such by systematists. Thus I have in my cultures at the present time numerous forms, some of which have originated through crossing, yet which breed fairly true and differ from each other quite as much as do the ordinarily accepted species in many genera, others which differ to a much slighter extent or even in single characters. For breeding purposes many of these various races urgently require description and a name by which one can refer to them. Such races should be grouped around the recognized species to which they are most nearly allied. If *cult.* be written after the names of such races, this will avoid the danger of seriously confusing them with the wild forms, while leaving open the question whether their differences are of specific, varietal, or lesser value. At the same time, this will not relieve systematists from the duty of examining all such descriptions, and according specific rank and treatment to any forms which, by their distinctness, deserve it, regardless of whether they originated in cultivation or elsewhere.

It will be easy to raise numerous objections to these suggestions, but it is believed that they will at least serve the purpose of making clearer the status of the many forms which must perforce be described by experimental workers before any permanent record of such experiments can be made.

The adoption of the term *mut.* as a designation for mutations whose origin is experimentally known, will, I believe, be particularly useful.

II. Conspectus of Species and Mutations of the *Onagra* group of *Oenothera*.

O. grandiflora, Solander* -------- *O. Tracyi*, Bartlett.
O. MacBrideæ, Nels.
O. macrosceles, A. Gray.

O. Lamarckiana, Ser. cult. ⟶
- *O. cognata*, Hort. Panorm. cult=seq.
- *O.* mut. *gigas*, H. DeVr. ⟶ *O.* mut. *gigas nanella*.
- *O.* mut. *rubrinervis*, H. DeVr. ⟶ *O.* mut. *rubricalyx*, Gates.
- *O.* mut. *lata*, H. DeVr. ⟶ *O.* mut. *lata nanella*.
- *O.* mut. *semilata*, H. DeVr.
- *O.* mut. *oblonga*, H. DeVr.
- *O.* mut. *scintillans*, H. DeVr. ⟶ *O.* mut. *scintillans nanella*.
- *O.* mut. *elliptica*, H. DeVr.
- *O.* mut. *albida*, H. DeVr.
- *O.* mut. *leptocarpa*, H. DeVr.
- *O.* mut. *fatua*, H. DeVr.
- *O.* mut. *spathulata* H. DeVr.
- *O.* mut. *sublinearis*, H. DeVr.
- *O.* mut. *subovata*, H. DeVr.
- *O.* mut. *nanella*, H. DeVr. ⟶
  - *O.* mut. *nanella oblonga*.
  - *O.* mut. *nanella elliptica*.
  - *O.* mut. *nanella lata*.
  - *O.* mut. *nanella scintillans*.
- *O.* mut. *laevifolia*, H. DeVr. ⟶
  - *O.* mut. *laevifolia salicifolia*.
  - *O.* mut. *laevifolia nanella*.
  - *O.* mut. *rubrinervis*?
- *O.* mut. *brevistylis*, H. DeVr.

var. *cruciata*.

O. Jamesii, Torr. & Gray.
O. argillicola, MacK.
O. Hookeri, Torr. & Gray.
O. Drummondii, Hook.
O. Simsiana, Ser.
O. ornata, Nels.
O. biennis, Linn.
O. canovirens, Steele.
O. Oakesiana, Robbins.
O. rhombipetala, Nutt.
O. strigosa, MacK. & Bush.
O. cheradophila, Bartlett.
O. muricata, Linn.
—— var. *canescens*, Robinson.
O. ammophila, Focke (an sp.?).
O. parviflora, Linn.
—— var. *cruciata*, Nutt.
O. Heribaudi, Lévl.

* As I pointed out elsewhere (Gates, 1911 *d*, p. 588), Solander rather than Aiton should be credited with the description of this species.

Key to Oenothera *species of the* Onagra *group.**

Petals cruciate, narrow and linear.
Cruciate varieties of *O. Lamarckiana* and *O. biennis* are described in DeVries, 'Die Mutationstheorie,' ii. pp. 593–633.

Petals broad; flowers large (petals 30–60 mm. long).
Style short, so that the stamens surround the stigma in the bud; flowers about 7 cm. in diameter, petals 4 cm. long . . . . . *O. Simsiana.*
Style long, so that the flowers are not self-pollinated in the bud.
Stems decumbent; plants clothed with soft pubescence, or canescently strigose.
Leaves ovate-elliptical or oblong, rather obtuse . . . . . *O. Drummondii.*
Leaves oblong-lanceolate, repandly denticulate, acute . . . . . *O. Jamesii.*
Stems erect, more or less muricated; flower-buds nearly or quite glabrous, bearing few or no long muricate hairs. Leaves usually more or less ciliate and pubescent.
Rosette-leaves narrowly oblanceolate, tapering above the acute apex.
Stem-leaves smaller, passing into sessile bracts . . . . . *O. MacBrideæ.*
Rosette-leaves spatulate-lanceolate with long petioles. Stem-leaves subsessile, oblong-lanceolate . . . . . *O. macrosceles.*
Rosette-leaves oblong-spatulate, tapering at the irregularly pinnatifid-toothed base into a long, broad petiole. Stem-leaves ovate-lanceolate, tapering at both ends, denticulate, blade passing below into a short, margined petiole . . . . . *O. grandiflora.*
Rosette-leaves broadly linear to linear-spatulate, sinuate. Stem-leaves undulate or repand-denticulate, linear to linear-oblong . . . . . *O. argillicola.*
Stems erect, muricated. Flowers not glabrous, but rather densely covered with muricated hairs.
Leaves canescently pubescent, plane, rather narrowly lanceolate, sessile, obscurely denticulate . . . . . *O. Hookeri.*
Leaves and usually buds less pubescent (fewer muricated hairs) . . . . *O. Lamarckiana* and [its segregates.

Petals broad; flowers smaller (petals about 12–30 mm. long).
Style exceeding the stamens. Leaves narrowly oblong-lanceolate to linear-lanceolate. Calyx densely white hirsute-pubescent . . . . . *O. ornata.*
Style short, not reaching beyond the anthers in the bud.
Sepal tips spreading; rosette-leaves narrowly lanceolate, approximately toothed at the acute apex, more deeply toothed at the slender, tapering base. Seeds large . . . . . *O. Oakesiana.*
Sepal tips appressed; plant annual, with evanescent rosette of a few small, red-spotted leaves, closely resembling *O. grandiflora.* Stem-leaves lanceolate, remotely denticulate, acute at both ends . . . . . *O. Tracyi.*
Sepal tips appressed; plant biennial. Lower stem-leaves 15–20 cm. long, elliptic-oblanceolate to elliptic-lanceolate, shallowly toothed, and often jagged-toothed near base, acuminate. Free sepal tips about 2 mm. long . . . . . *O. biennis.*

---

* I am indebted to Sir David Prain, F.R.S., Director of the Royal Botanic Gardens, Kew, for permission to examine the list of *Oenothera* species in the next (unpublished) supplement to the 'Index Kewensis.'

Sepal tips appressed; plant biennial. Stem-leaves numerous and crowded, excurved-ascending, lower leaves 9–10 cm. long, lanceolate-oblong, tip very acute; petiole and midvein broad, the latter somewhat succulent. Leaves densely cinereous-pubescent, blue-green	*O. canovirens.*
Petals rhombic-ovate, 12–25 mm. long. Stem-leaves narrowly lanceolate, acuminate, denticulate or subentire	*O. rhombipetala.*
Petals 15–20 mm. long, light yellow; sepal tips 3 mm. long. Plants strigose and somewhat villous; stigma-lobes flattish, spreading . .	*O. strigosa.*
Petals 9–15 mm. long; leaves narrow in most races but broad in certain races	*O. muricata.*
Whole plant hoary-pubescent or somewhat silky	var. *canescens.*
Petals about 8 mm. long.	
Sepal tips about 3 mm. long, style short, petals broad (9 mm.) . . .	*O. parviflora.*
Sepal tips about 3 mm. long, style short, petals cruciate	var. *cruciata.*
Sepal tips less than 1 mm. long, style short, petals broad; stigma-lobes teretish, ascending	*O. cheradophila.*
Petals lanceolate, style long, foliage soft-pubescent	*O. Heribaudi.*

The following salient features of these species, as far as they can be judged from present knowledge, may be pointed out:—

O. Simsiana is sharply distinguished by its large flowers with short style.

O. Drummondii and *O. Jamesii* have more or less decumbent stems, the former being very distinct with its short, ovate-elliptical leaves; the latter nearly agreeing with *O. Lamarckiana* in foliage characters, but apparently differing chiefly in its decumbent stem and greater pubescence.

O. MacBrideæ is apparently nearest to *O. grandiflora*, from which it differs chiefly in its narrower leaves and somewhat shorter style *.

O. macrosceles comes nearest *O. Jamesii* and *O. Lamarckiana* in foliage, but differs from the former in its upright stem, and from both in being nearly glabrous.

O. argillicola is sharply set apart from *O. grandiflora* by its very narrow, linear-oblong leaves.

* Since the above was written I have been able, through the kindness of Professor Nelson, who sent me seeds, to grow this species and study its characters. The following notes are appended from my observations on this species.

Cotyledons very long and narrow, twice the length of related forms. Rosettes of characteristic rather broadly lanceolate-oblong leaves. Central stem erect, surrounded by many long spreading branches from the rosette. Cauline leaves long and narrow, pointed, pale green, midrib white, surface smooth, margin repand-denticulate. Hypanthium, bud-cone, and ovary closely set with long hairs arising from faint red papillæ. Sepals pale pink with touches of red on the hypanthium, sepal tips short and closely appressed. Petals 44 mm. long by 52 mm. broad, emarginate, length of bud-cone 40 mm., diameter of cone at base 9 mm., length of hypanthium 48 mm., ovary 19 mm., sepal tips 4 mm., thickness of ovary 3–3·5 mm., thickness of hypanthium 3 mm. Base of stigma usually some distance above the stamens.

The buds of these plants were apparently not so nearly glabrous as one might judge from Nelson's description. The plants do not resemble *O. grandiflora* closely in buds or in foliage, nor do they come in the *biennis* series, since they have larger flowers and longer styles.

Oenothera Hookeri differs from *O. Lamarckiana* and its mutants in its canescent pubescence and the absence of crinkling in the leaves.

O. ornata apparently forms a transition to the smaller-flowered *O. biennis* forms, though its style exceeds the stamens. It appears to differ from the latter in its denser hirsute-pubescence and somewhat larger flowers with longer style.

O. Tracyi in general characters agrees closely with *O. grandiflora*, from which it differs chiefly in its smaller flowers with short style.

O. biennis as now understood has leaves long, elliptic-oblanceolate to elliptic-lanceolate, shallowly toothed and frequently with jagged teeth near the base. The petals vary from 12–25 mm. long.

O. Oakesiana differs from *O. biennis* in foliage, but also in having spreading sepal tips and large seeds.

O. canovirens, another segregate from *O. biennis*, differs from that form markedly in foliage, the petioles being somewhat succulent, the leaves much shorter, densely cinereous-pubescent, and blue-green.

O. rhombipetala differs from *O. biennis* in foliage, but chiefly in having rhombic-ovate petals.

O. strigosa differs from *O. biennis* chiefly in being strigose, the foliage variable.

O. cheradophila differs from *O. strigosa*, which it most resembles, chiefly in having much smaller flowers (petals 8 mm. or less) with shorter sepal tips.

O. muricata differs constantly from the *O. biennis* series of forms in having smaller flowers (petals 9–15 mm. long). Most of the races also have narrow leaves, but certain ones have broad leaves.

O. parviflora has still smaller flowers than *O. muricata* (petals 8 mm. long). It also differs in foliage characters.

O. Heribaudi agrees with *O. parviflora* in flower-size. It has the habit of *O. biennis*, but has a long exserted style, and its foliage resembles that of *O. sinuata*, a form which does not come strictly within the *Onagra* group.

It is a matter of opinion how far *O. Oakesiana*, *O. canovirens*, *O. rhombipetala*, *O. strigosa*, *O. cheradophila* and similar segregates from *O. biennis* should be recognized as distinct species. "Splitters" will recognize many at least as such, while others, such as Lévéillé in his monograph of the genus, will "lump" them all as races of one species. That these different races will breed true there can be no doubt. Indeed, even smaller differences remain constant in cultures.

III. Relationships of Species.

General Distribution.—The genus *Oenothera* is well-known to be exclusively American in origin, although in the last three centuries, since its introduction into European Botanical Gardens, it has escaped and is now naturalized and growing wild in many parts of the world. In England, large-flowered forms related to *O. Lamarckiana* are known to have been growing in great numbers on the Lancashire coast since at least 1806 and probably much earlier. (Smith, in Sowerby, English Botany, vol. xxii.

pl. 1534.) They are also found in various other parts of England, and are widely distributed, particularly on sand-dunes and along railway-lines in France, Germany, Holland, and in fact all over Europe. They also occur in such regions as the Azores, South Africa, Australia, Japan, &c., and I have obtained new races with unexpected characters in cultures of seeds from some of these localities. The origin of such races is a problem of much interest, and may furnish important data on the question of the effects of climate in the origin of races. It is very desirable that detailed studies of naturalized colonies of Oenotheras in various parts of the world should be undertaken.

Specific Differences.—The species with which the students of the mutating Oenotheras have been chiefly concerned are *O. Lamarckiana*, *O. grandiflora*, *O. biennis*, and *O. muricata*. An analytical key (Gates, 1909 *c*) gives the main distinguishing features of these species and their segregates and relatives, and subsequent papers (Gates, 1911 *a*, 1911 *d*) have traced the history of the origin of these names as they were applied to races introduced into European Gardens. It seems desirable to point out that after long familiarity with these forms I find it necessary to conclude that the limits between the species are purely arbitrary. Fixed limits can only be maintained as a matter of convenience in dealing with a host of forms. For races are found which overstep any boundary-line which can be drawn between each species and those to which it is most closely related. The type of each species is only one of many related races which have come to be included with the type in systematic descriptions. Which of these races originally received the name of a given species was purely a matter of chance, because it was the first to come under the botanist's notice. But while these types furnish useful landmarks, yet, when whole series of additional races are observed, they must either be given new specific names or classed as races under certain species already described. The advisability of giving specific rather than racial names to these newer-discovered forms will not be discussed here, but it is sufficiently clear that names of some sort are necessary in dealing with them, either from the standpoint of a more complete knowledge of the flora of any country, or from that of the evolutionary experimentalist who must have names to designate the various forms with which he works. When these forms differ in single characters, such as flower-colour, which can be described in one word, that word is all that is necessary for a name. But when such geographic races differ slightly in many characters affecting leaf, stem, flower, and fruit, as in *Oenothera*, the necessity for an accurate description and a name for each such race is sufficiently evident, and is highly desirable both from the systematic and the breeding point of view.

Since, therefore, more or less arbitrary lines of distinction between the species are necessary I have, for convenience, adopted the following:—*O. Lamarckiana* and *O. grandiflora* forms nearly agree in flower-size, but the latter have no long muricated hairs, or very few, on their sepals, while the former possess at least a considerable number. The *O. grandiflora* races are also characterized by possessing rosette-leaves with deep basal lobes, while these do not occur in the known *O. Lamarckiana* races. The *O. biennis* races differ from the two previous groups only in having smaller flowers

(diameter about 3 cm.) with short style, so that the anthers surround the stigma and self-pollination takes place in the bud. The many wild races of *O. biennis* differ widely in leaf-characters and vary somewhat in size of flower. The races of *O. muricata* have smaller flowers with usually shorter style than *O. biennis*. This is the only distinction which can be drawn which will apply to all known races. Many narrow-leaved races of *O. muricata* occur, but certain races have broad leaves as well as small flowers, so that the latter character alone is retained as delimiting this group of races (see Gates, 1911 *d*, p. 580).

Below are represented the lines of difference which may be drawn between these four species and their relatives and segregates :—

1. Flowers large (length of petals 35–50 mm.). Style long and flowers open-pollinated (except in *O. brevistylis*, *O. Simsiana*, and certain other forms).	
a. Buds smooth or bearing only short hairs, rosette-leaves usually having basal lobes	*O. grandiflora* races.
b. Buds bearing also long, pointed hairs, which arise from papillæ . . .	*O. Lamarckiana* races.
2. Flowers small (length of petals 15–25 mm.). Style short, causing self-pollination	*O. biennis* races.
3. Flowers smaller (length of petals 9–15 mm.). Style short, flowers self-pollinated	*O. muricata* races.

Before proceeding to an examination of their characters and behaviour let me outline the history of some of these races and their present distribution in America.

History of Races.—I have devoted considerable attention (Gates, 1911 *a* and 1911 *d*) to the history of the introduction of Oenotheras from America into Europe, tracing the records of the individual races since the first introduction in 1614, as far as possible from the early names, plates, herbarium specimens, and descriptions. Some of the main conclusions may be mentioned here in condensed form. The earliest *Oenothera*, of which there is any record, was brought to Europe probably in 1614 and grown in the Garden at Padua. In 1619 C. Bauhin grew this race from seeds obtained from Padua, and the species is described in the Appendix to Bauhin's 'Pinax,' page 520 (1623). Bauhin's original specimen no longer exists, but the evidence from all sources, though inconclusive, indicates that this first introduction, which Bauhin named *Lysimachia lutea corniculata*, was a type of *O. biennis*, now wild in Europe, and having larger flowers than the American races of *O. biennis* now known, but smaller than *O. Lamarckiana* or *O. grandiflora*. Afterwards various independent introductions and descriptions of Oenotheras were made from time to time, and some of the data regarding their names, origin, and probable identity are given in the following table. In some cases it seems impossible to be certain regarding the identity of the plant described or illustrated. But in a few instances comparisons are made or other data provided which make the determination at least very highly probable. Thus the figure and description of *Lysimachia Americana* by Columna leaves considerable doubt regarding its identity, though the plant may perhaps have come from the same source as Alpino's *Hyoscyamus*

TABLE I.—*Early references to* Oenothera.

Date.	Place.	Name.	Author.	Work.		Probable identity of Species.
1614.	Padua?,	Seeds from Virginia.				
1619.	Basil.	*Lysimachia lutea corniculata.**	C. Bauhin.	Pinax, pp. 245, 520.	Description.	"European *O. biennis.*"
1627.	Venice.	*Hyoscyamus Virginianus.* †	Alpino.	De Plantis Exoticis.	Description and plate.	,, ,,
1628.	Rome.	*Lysimachia Americana.* ‡	Columna in Hernandez.	Nova Plant., Anim. et Miner. Mexicanorum.	,, ,,	,, ,,
1629.	London.	*Lysimachia lutea siliquosa Virginiana.* §	Parkinson.	Paradisus.	,, ,,	,, ,,
1640.	,,	,, ,, ,,	,,	Theatrum Botanicum.	,, ,,	,, ,,
1669.	,,	*Lysimachia corniculata minor lutea Canadensis.*	Morison.	Hort. Reg. Blesensis.	Description.	*O. muricata.*
1669.	,,	*Lysimachia lutea flore globoso,* Park. Ger.	,,	,, ,,	,,	*O. fruticosa.*
1680.	Oxford.	*Lysimachia lutea corniculata non papposa Virginiana major.*	,,	Plant. Hist. Univ. Oxon., ii.	,,	—
		Lysimachia lutea corniculata non papposa Virginiana minor.	,,	,, ,,	,,	—
1680.	,,	*Lysimachia Virginiana latifolia lutea corniculata.*	,,	,, ,,	Plate.	*O. biennis.*
1680.	,,	*Lysimachia Virginiana angustifolia corniculata.*	,,	,, ,,	,,	*O. muricata.*
1686.	London.	*Lysimachia lutea Virginiana.*	Ray.	Historia Plantarum, i.	Description.	European *O. biennis.*
1686.	,,	*Lysimachia Virginiana altera, foliis latioribus, floribus luteis, majoribus.*	,,	,, ,,	,,	*O. grandiflora* or *O. Lamarckiana.*
1694.	Paris.	*Onagra latifolia.*	Tournefort.	Élém. de Botanique.	Listed.	European *O. biennis.*
1694.	,,	*Onagra angustifolia.*	,,	,, ,,	,,	*O. biennis.*
1694.	,,	*Onagra angustifolia, caule rubro, flore minori.*	,,	,, ,,	,,	*O. muricata.*
1700.	,,	*Onagra latifolia, floribus amplis.*	,,	Institutiones Rei Herbariæ.	,,	*O. grandiflora.*
1714.	,,	*Lysimachia latifolia, spicata, lutea Lusitanica.*	Barrelier.	Plantæ per Gall., Hisp. et Italiam observatæ.	Plate 989.	*O. biennis.*
1714.	,,	*Lysimachia angustifolia, spicata, lutea Lusitanica.*	,,	,, ,,	Plate 990.	*O. muricata.*
1714.	,,	*Lysimachia lutea, corniculata, latifolia Lusitanica.*	,,	,, ,,	Plate 1232.	*O. grandiflora* or *O. Lamarckiana.*
1760.	London.	*Oenothera foliis lanceolatis, dentatis, caule hispido.*	Miller.	Figures of plants described in the 'Gardener's Dictionary.'	Plate.	*O. muricata.*
1760.	,,	*Oenothera foliis ovato-lanceolatis planis.*	,,	,, ,,	,,	*O. biennis.*

* Seeds from Padua.
‡ ,, ,, Johannes Pona in Verona.
† Seeds from an English physician.
§ ,, ,, Virginia.

Virginianus. But there can be no doubt that Ray's *Lysimachia Virginiana altera, folius latioribus, floribus luteis majoribus* is a large-flowered form, though there are no data to decide whether it belongs in *O. grandiflora* or *O. Lamarckiana*. Similarly, Barrelier in 1714 gives figures of three species of *Oenothera* which can be identified with practical certainty as (1) *O. biennis*, (2) *O. muricata*, and (3) *O. grandiflora* or *O. Lamarckiana*, the last figure applying perhaps equally to either of these species.

The facts which emerge are that a large-flowered Virginian form, which must have belonged in the *grandiflora-Lamarckiana* series, was recognized as early as 1686 by Ray, while *O. muricata* was recognized in 1700 by Tournefort and figured by Barrelier in 1714, together with *O. biennis* and the large-flowered form. Curiously enough, the large-flowered Oenotheras seem to have been lost from English Gardens, for Bartram in 1778 re-discovered *O. grandiflora*, this time in Alabama, and it then was introduced into England and received its modern name. But *O. grandiflora* is now known to have survived in Virginia and Carolina as late as 1820, so that there can be no doubt that the early introduction before 1686 was of a race belongiug to *O. grandiflora* or *O. Lamarckiana* from Virginia. *O. grandiflora*, therefore, had two introductions into England, one from Virginia and one from Alabama, unless (as is equally probable but not provable) the earlier introduction was *O. Lamarckiana*. In 1796, some years after the introduction from Alabama, *O. Lamarckiana* was recognized in Paris as distinct from *O. grandiflora*, and thus it had its taxonomic origin. It had long been going under the name *O. biennis*. As late as 1860 *O. Lamarckiana* was again introduced into England, this time from Texas, and the plants of DeVries's cultures are descended from this source. It seems, therefore, certain that the naturalized plants on the Lancashire sand-dunes (which contain both *O. Lamarckiana* and *O. grandiflora*) had an independent and much earlier origin, yet the *O. Lamarckiana* characters in both cases agree even to the point of identity.

Of course the question of the origin, introduction into cultivation, and identity of *O. Lamarckiana* has furnished the most absorbing part of this historical work. Has *O. Lamarckiana* originated in Europe or America? Is it a hybrid produced in Botanical Gardens by spontaneous crossing, and, if so, what remains of DeVries's mutation theory? I have pointed out elsewhere (Gates, 1911 *d*) that all the hereditary behaviour of *O. Lamarckiana* cannot be explained as the result of hybrid splitting. I have also pointed out that if *O. Lamarckiana* originated as a result of crosses between *O. grandiflora* and *O. biennis* in European gardens, the same thing must have happened long previously in the Virginia-Carolina region, where both were certainly originally indigenous. But I have further pointed out that it is of little moment whether *O. Lamarckiana* originated from crosses on this side or the other side of the Atlantic, for it is self-evident that in such open-pollinated forms as *O. Lamarckiana* and *O. grandiflora*, crossing of races must be continually occurring in nature. This is, in fact, one of the conditions under which the evolution of any open-pollinated group of forms must take place. We must, therefore, assume a mixed ancestry for *O. Lamarckiana* in any case, many closely related races having taken part in that ancestry. But there is no

evidence that *O. Lamarckiana* is in this sense any more "impure" than *O. grandiflora*. Further, while there is no indubitable evidence that *O. Lamarckiana* was introduced from America previous to 1686 having just the characters it has now, yet I can find no reason for supposing that the large-flowered plants of Ray (1686), Tournefort (1700), and Barrelier (1714) belonged any nearer to *O. grandiflora* than to *O. Lamarckiana*.

The fact that *O. Lamarckiana* has not been found wild in North America during the last half-century cannot be used as a valid argument for its origin as a hybrid in European Gardens, for several reasons. (1) Certain races of *O. biennis* also are now known only in Europe and seem to have disappeared from America. (2) It is evident that, at least in the Eastern States, which have been longest settled, the open-pollinated forms such as *O. grandiflora* have become practically extinct since the introduction of civilization, while the self-pollinating *O. biennis* and *O. muricata* races are still found abundantly in the East as well as the West. This might be anticipated, for in self-pollinated plants, flowering is sure to be followed by seed-production, while in open-pollinated species the flowers are often very imperfectly pollinated. Hence, with the increasing enemies resulting from the advent of civilization, species such as *O. grandiflora* and *O. Lamarckiana*, which are open-pollinated, would soon reach a condition in which their seed-production was insufficient to maintain the race, while plants with the close-pollinating habit would not be adversely affected. That the close-pollinated species of *Oenothera* produce many more seeds than the open-pollinated when left to themselves under the same conditions, is a matter of direct observation in my own cultures, so that it is not surprising that in the Eastern States, which have been longest occupied by civilized man, the open-pollinated species should have become extinct.

On the other hand (3) many open-pollinated forms still remain in the Western States, which are more recently and less densely populated. As recently as 1867 a specimen was collected in Colorado (see Gates, 1911 *d*, p. 589) which appears almost identical with *O. rubrinervis*, a mutant from *O. Lamarckiana*. A new species (*O. ornata*), evidently closely related to *O. grandiflora*, was described from Idaho only last year (Nelson, 1911). It is evident, then, that forms at least very closely related to *O. Lamarckiana* are still to be found in the Western States, and there remains at present no sufficient reason for assuming that *O. Lamarckiana* originated only in cultivation. Its mixed ancestry, on the other hand, must be admitted by all who carefully consider the question. But this condition it shares with *O. grandiflora*, *O. Hookeri*, and indeed with all open-pollinated plants in which mongrel races are fertile.

As regards the original distribution of these species in North America, it seems quite evident that the large-flowered forms, including both *O. grandiflora* and *O. Lamarckiana*, originally extended from the Eastern Atlantic region of "Virginia" westward to Texas, and it is certain that *O. grandiflora* extended at least from Virginia to Alabama. The physiological behaviour of this species in cultures indicates that the race now surviving in Alabama is adapted to a somewhat more southern climate than *O. Lamarckiana*. It is stated, however (Macoun, 1883, p. 171), that *O. grandiflora* is common in Ontario. I have not seen this form to determine its exact characters. From the data

now at hand from numerous collections of wild seeds from all over the continent, as well as from other facts, it seems that though the three species *O. grandiflora*, *O. biennis*, and *O. muricata* very largely overlap in their distribution, yet *O. grandiflora* is on the whole the most southern and *O. muricata* the most northern. I have collected identical races of *O. muricata* from Nova Scotia, New Brunswick, and Manitoba, so that the decrease in flower-size in the more northern latitudes may not be devoid of significance.

IV. Variations and Mutations of *O. Lamarckiana*, Ser.

Since the important researches of DeVries, covering many years' experiments, in which he showed that a group of divergent types arise from *O. Lamarckiana* when it is cultivated in large nnmbers, the need of a more detailed analysis of this behaviour has become evident. The idea of recurring "mutation periods" as accounting for this behaviour has not found universal favour with biologists, and there is no detailed evidence in its support. It is probable that the premutation hypothesis of DeVries will also be found untenable. Indeed, the author's own views on some of these subjects have probably changed since the publication of 'Die Mutationstheorie' in 1901. But a satisfactory hypothesis as to why the aberrant types appear has not been given. From the facts presented in previous papers and briefly summarized in the last section, it will appear that the mutation phenomena in *O. Lamarckiana* are closely connected with the crossing which has taken place in its ancestry, but, so far from depriving these phenomena of significance, they show rather that the species-unit in open-pollinated plants is much more complex than was previously realized. *O. Lamarckiana*, *O. grandiflora*, and *O. Hookeri* are all undoubtedly "hybrids," if by that is meant forms whose ancestry has undergone crossing, and has therefore been contributed to by several rather closely related races. But in this connection several things must be kept in mind: (1) That the mutants which appear in each generation probably are not the same as the races which contributed to the ancestry of the species; (2) that *O. Lamarckiana* itself shows much more variation in different cultures (races) than has previously been supposed; (3) that (as I shall show) the mutants themselves frequently exhibit a wide range of variation, in some cases much wider than would be supposed from the previous accounts of this mutation process.

In the following account I shall endeavour to exhibit the range of fluctuating variation of *O. Lamarckiana* itself and of its various mutants. It is important to remember, on the other hand, that, although some of the races frequently overlap in their variability (so that an apparently continuous series can be formed from them), yet they are really discontinuous in origin, as evidenced by their behaviour when inbred or crossed. Another important point, which has been neglected in previous studies of these forms, is the series of ontogenetic stages passed through by the rosettes in their development. Successive leaf types appear, which often differ from each other to a striking degree, so that different stages of the same rosette may be much more unlike than corresponding stages of rosettes belonging to different races. In the study of

hybrids it is particularly important that the hybrid offspring should be compared with each other, and with their parents in every stage of their ontogeny, and not merely in the end stages. It is also essential that care be exercised to compare corresponding stages of the rosettes, for misleading conclusions may arise from a comparison of rosettes of different ages. Nowhere is the necessity for taking account of all the ontogenetic stages of organisms more apparent than in such forms as the Oenotheras, where a number of different types of leaf succeed each other in the development of the individual. Indeed, in *Oenothera*, from the first seedling leaf to the fully developed rosette and the mature flowering plant, there is a constant succession of changes in leaf-shape. The cotyledons also pass through a regular series of changes in shape and size after they first appear.

The following series of photographs is offered in proof of some of these statements. They are selected from a much larger number, which have accumulated in connection with the records of my experiments. Pl. 1. fig. 1 shows a pan of young seedlings of *O. Lamarckiana*. They are very uniform, but are developing at different rates. Figs. 25, 21, and 15, which show respectively *O. rubricalyx*, *O. brevistylis*, and *O. laevifolia* at the same age, should be compared with this. The comparison will show that even the young seedlings are sharply distinct from each other in shape of leaf-blade and length of petiole. The crinkling of *O. Lamarckiana* may appear in even the earliest leaves following the cotyledons.

It should be pointed out that *O. Lamarckiana* is by no means the only *Oenothera* having crinkled leaves. An equal amount of crinkling is to be observed in a race of *O. biennis* from the Chelsea Physic Garden, which I have grown for several years. Such mutants as *O. lata* and *O. nanella* show as much or more crinkling than *O. Lamarckiana*, while nearly all the mutants (even *O. laevifolia*) show more or less of it.

The suggestion of DeVries (1909, i. p. 309) that the crinkling is due to faulty correlation between the growth of the veins and of the areas of mesophyll between them, appears to be correct, and is supported by the fact (referred to elsewhere in this paper) that in certain dwarf plants the reduction in the dimensions of the vessels of the stem is more or less independent of the change in size of the cortical cells.

Pl. 1. fig. 2 is a photograph of a rosette of *O. Lamarckiana* about four months old—*i. e.*, four months after the seeds were sown. Fig. 3 shows a similar rosette of *O. Lamarckiana* at about the same stage of development, grown in heavy clay soil. Under these conditions the development of the rosette is slow, and the various types of rosette-leaves can be carefully followed as they appear. In this way it is found that three distinct types of rosette-leaf successively make their appearance:—(1) Narrow type of leaf, smooth, entire and oblong, with rounded tip: two leaves of this type are present in fig. 3; this is followed by (2) a cycle of three leaves, broad, nearly smooth, with very obtuse tips, narrowed abruptly to the petiole, longer than (1); then after one or two transition leaves appears (3) the type of leaf of the mature rosette. These are

longer and narrower than (2), usually much crinkled, pointed, the blade narrowed gradually to a petiole with irregularly lobed or jagged margin. In fig. 4, which is a little further developed, the same three types of leaves are found. Figs. 3 and 4 should be compared with fig. 13, Pl. 2. figs. 14 and 16, which show that the *O. lævifolia* rosette passes through the same series of developmental stages as *O. Lamarckiana*. Indeed, these three figures are. perhaps, indistinguishable from figs. 3 and 4 of *O. Lamarckiana* in photographs, yet the earlier stage (fig. 15) of *O. laevifolia* is plainly different from the corresponding stage of *O. Lamarckiana* (fig. 1). From such facts one learns that types which are at first divergent may converge during development, and later diverge again so that the adults are as unlike as the young seedlings. In *Oenothera*, as the plants grow, such changes are constantly going on, and they add much to the complexity of the facts, and greatly increase the necessity for the most detailed observation and comparison of the individual plants in all the stages of their ontogeny. The necessity for this becomes particularly strong in dealing with hybrids.

After the third type of rosette-leaf appears there follows a continuous succession of leaves of this type, the leaves of each cycle being longer than those of the preceding cycles (though otherwise the same), until a maximum diameter of the rosette is reached (Pl. 1. fig. 5). After this, if the rosettes of *O. Lamarckiana* or its derivatives are kept under constant conditions of high temperature and high moisture content, leaves of the same type continue to appear, the older ones dying away below, until a considerable area of stem may be formed without internodes (see Gates, 1912). The plants will usually continue to produce rosette-leaves as long as these tropical conditions are prolonged. Under ordinary conditions of culture, however (in which the seeds are sown in pans in January, the seedlings afterwards transplanted to pans in the greenhouse, and the young rosettes planted out-of-doors in May), a stem soon begins to form. The lower cauline leaves form a somewhat abrupt transition from the rosette-leaves. As observable from figs. 7 and 8, the upper stem-leaves are sessile or nearly so, with a broad, more or less aurate base, and they diminish gradually but strongly in length and width in passing up the stem. The lowermost stem-leaves have long petioles and elongated blades like the rosette-leaves, but these quickly change above to the cauline type of leaf having a very short petiole and shorter, aurate blade. The leaves of the whole organism therefore form a continuous series, whose continuity is, however, broken by rather sharp transitions at two places in the rosette development, and also in the passage from radical to cauline leaves. In Oenotheras of the *Lamarckiana* group there is, under the conditions of my cultures, a considerable pause after the maximum diameter of the rosette is reached, during which further cycles of rosette-leaves of the same type continue to be produced, before elongation of the stem begins.

In Pl. 1. fig. 6 are shown six leaves selected from typical mature rosettes of *O. Lamarckiana* at this time, to show the range of variation in the length, width, and pointedness of the leaves at this stage. With this should be compared Pl. 2. figs. 18 and 23, selected respectively from *O. laevifolia* and *O. brevistylis* to show their ranges of variability in the same stage of development. It will be seen that if the leaves of all

three were mixed indiscriminately they would form a perfectly continuous series, both as regards width of blade and breadth of leaf-tip. In other words, the three series of leaves clearly overlap in the ordinary range of their variability, for they were not selected from extreme individuals but from representative members of each type of mature rosette. Yet it is equally clear that this is not really a case of continuous variation, for *O. laevifolia* produces narrower leaves than ever occur in *O. Lamarckiana*, and *O. brevistylis* contains leaves with broader, more obtuse tips than ever occur in *O. Lamarckiana*. But of much more importance is the fact that the modal condition for width of leaf and breadth of tip is different for each species. Shull (1907, p. 22) has shown statistically that the modal condition of *O. Lamarckiana* and *O. rubrinervis* shows constant differences for several characters.

It is true that there is a certain amount of individual variability within each race—for example, the leaves of the mature rosette will be, on the average, narrower in certain individuals than in others; but it is not often that all the leaves of a rosette are of such character that the plant cannot be determined with reasonable certainty at this stage, although occasional cases of transgressive variability occur between most of the forms, which render the determination of such individuals indecisive until a later stage of their development. Such cases occur in which, for instance, rosettes of *O. laevifolia* or *O. rubrinervis* or *O. brevistylis* cannot be distinguished from *O. Lamarckiana*, or *vice versa*. But it must be said that such cases are not common. That each of these forms has a different modal condition for its various leaf-characters is perfectly clear and indisputable, even though transgressive variability or fluctuation occasionally asserts itself with regard to any of these characters in particular individuals.

Pl. 1. figs. 7 and 8 are photographs of adult plants of *O. Lamarckiana*, showing the range of variability in the crinkling of the leaves. The individual in fig. 7 has an exceptional amount of crinkling, this feature being almost as fully developed as in *O. lata*, though the leaves are longer and more pointed than in that mutant. Fig. 8 marks the other extreme, in which the upper stem-leaves are practically devoid of crinkling. This is much nearer the modal condition of *O. Lamarckiana* than the previous figure, for the upper stem-leaves usually have very little crinkling.

These figures give a fair idea of the range of fluctuating variability in cultures of *O. Lamarckiana* derived from seeds of DeVries. I have since had experience with races of *Oenothera* from other sources, which, although they are undoubtedly to be included in the species *O. Lamarckiana* in the strictest sense, yet differ quantitatively in nearly every character from the *O. Lamarckiana* race of DeVries's cultures, even when grown side by side with them under the same environmental conditions for several generations *. A study of certain of these races, and a comparison of their characters through several generations with those of the *O. Lamarckiana* of DeVries's cultures, shows that such quantitative differences, however they may have arisen, continue to be transmitted, so that the races remain strictly differentiated. I am inclined to believe that this fact of the strict inheritance of quantitative differences in various races of the same species may

* See also note, page 67.

prove to be one of the salient features of heredity in *Oenothera*, and may account for some of the almost bafflingly difficult phenomena to be observed among these forms.

The following represents the history of one such *O. Lamarckiana* race. It was derived from a single individual which appeared from an unknown source in the back-yard of a citizen of St. Louis, Mo., where no Oenotheras had previously been seen, so that its origin cannot even be conjectured. From pure seeds of this individual I grew in 1910 a uniform offspring of 38 plants. Fig. 9 shows the range of variation of the seedlings, which was not very great. The close similarity to DeVries's race of *O. Lamarckiana* (at a somewhat younger stage) is shown by comparing Pl. 1. fig. 1. Three plants of the F_1 were self-pollinated as parents for the next generation, and yielded respectively 62, 29, and 41 plants, making a total of 132 plants in the F_2. Pl. 1. figs. 10 and 11 show a typical rosette and adult plant for comparison with Pl. 1. figs. 5 and 8. The rosette-leaves of this race are crinkled similarly to the plants of DeVries's race, but they have decidedly broader leaves and the latter are conspicuously larger, so that the rosettes reach a much greater diameter. The individual leaves of the mature rosettes also show wider fluctuation than in DeVries's race. The stem-leaves of this race are also much more variable than in DeVries's form. The same individual may bear leaves ranging all the way from ovate, tapering at both ends, and petiolate (thus resembling *O. grandiflora*) to sessile or nearly so, with broad and aurate base (as is usual in *O. Lamarckiana*). These leaf types do not always form a definite transition series, but one type may be found chiefly on the main stem and the other on a side branch. Both rosette- and stem-leaves are, on the average, somewhat more crinkled than in DeVries's race, and the buds bear fewer long hairs. On the whole, the fluctuating variability of this race is decidedly greater than in the *O. Lamarckiana* of DeVries's cultures. This is, perhaps, due to the fact that continued inbreeding has decreased the range of ordinary variation in the latter race.

Among the 132 individuals of this race in the F_2, all belonged to the parent type but two plants which must be classed as mutants. One of these was a dwarf, corresponding to but not agreeing with *O. nanella*, the other a narrower-leaved one, corresponding to *O. rubrinervis*. This race of *O. Lamarckiana*, therefore, is capable of producing aberrant types analogous to, but not identical with, those described by DeVries: a fact of considerable interest. The following table summarizes these facts:—

TABLE II.

F_1.	F_2.		Mutants.
38 plants.	No. 3.5.	62 plants.	....
	No. 1.1.	29 „	1 narrow-leaved plant.
	No. 2.2.	41 „	1 dwarf plant.
		132 „	

Another race of *O. Lamarckiana*, whose characters differ only quantitatively from those of DeVries's race, I have studied carefully and compared with the latter. This race was derived from the coast near Liverpool and has already been referred to in connection with the history of *O. Lamarckiana* (see p. 18). Bailey (1907) showed that this form was *O. Lamarckiana*, and MacDougal (1907, p. 8) found from cultures that it produced several mutants. I have since made more detailed comparisons of forms from this locality, and have discovered a number of new forms, some of which have been isolated as races, and a few of which will be referred to in this paper. The *O. Lamarckiana* race from St. Anne's is almost identical with that of DeVries, being much closer than the last race described, yet there are a few quantitative differences in such features as width of rosette-leaves, diameter of rosette, and number of long hairs on the sepals, which appear to be constant.

I have seen one other race of *O. Lamarckiana* from this locality which differed considerably in the shape of its stem-leaves, which were longer and tapering to a petiole at the base. This race stood somewhat nearer to *O. grandiflora* in its characters. One may therefore expect to find races of *O. Lamarckiana* bridging more or less completely the gap between this species and *O. grandiflora*. A series of hybrids between certain races of *O. Lamarckiana* and *O. grandiflora*, which I am now cultivating in F_2, may throw some light on the origin of such intermediate races. For the F_1 contained two types each of which approaches one parent although in certain features resembling the other. The two hybrid races were therefore different from either parent, though intermediate.

Another very interesting race, which I received from the Bremen Botanical Garden under the name *O. Lamarckiana*, Ser., var. *cruciata*, must be briefly described here. In this culture 53 plants developed. Their rosette-leaves closely resembled *O. Lamarckiana*, being deeply crinkled, but frequently broader in the middle of the blade than typical for that form. Many leaves were also of rather larger size than *O. Lamarckiana* usually attains, the maximum size being $9{\cdot}5 \times 36$ cm. Of these rosettes, 11 showed a striking peculiarity which I have not seen in any other form * (see Pl. 1. fig. 12), and several others showed traces of it. The leaves were peculiarly curled and sickle-shaped, the blade being almost wholly undeveloped on one side of the midrib. There was no lack of chlorophyll and no evidence of any parasite, although it is possible the condition may be pathological. The peculiarity appears when the seedlings are less than two months old. I have not yet made the test, but it is probable that the peculiarity is at least partially inherited. The only case I have seen at all resembling this is a single rosette (see Gates, 1910, pl. 31) in a culture of an *O. Lamarckiana* from Lancashire. In this rosette many of the leaves were green on one side of the midrib and colourless (lacking chloroplasts) on the other. The colourless portion continually died away from lack of nourishment, but there was no curving around of the green half of the leaf. I interpreted that case as a probable sectorial chimera, but it is not probable that that explanation could apply in the present case.

The flowers of this race also presented several remarkable peculiarities. The style was

* I have since observed similar aberrations in certain other races.

short, so that nearly all the flowers were self-pollinated, and the petals were partly cruciate and partly normal on the same plant. Measurements showed ovary 11 mm.; hypanthium 35 mm.; bud-cone 20 mm.; free sepal tips 6 mm.; petals 30 mm. long; cruciate petals 7 mm. broad; normal petals 32 mm. broad; hypanthium very stout, 3·5 mm. in diameter.

In my cultures 737 plants of DeVries's race of *O. Lamarckiana* have been grown from pedigree seed. Of the larger cultures, 170 plants in 1907 gave one mutant *O. rubrinervis*, and 115 plants in 1909 gave two *O. lata* mutants. The remaining plants were in small cultures not exceeding 50 plants of each pedigree, and they produced no mutants.

O. laevifolia.

This species has never appeared as a mutant from *O. Lamarckiana*, but was found by DeVries in the locality at Hilversum from which his cultures of *O. Lamarckiana* were obtained. I have already referred to some of the differences from *O. Lamarckiana*. The leaves both of the adult rosette and the stem are distinctly narrower than in *O. Lamarckiana*, as seen from Pl. 2. figs. 16, 17, and 18; the latter, which shows the range of variation in width and amount of crinkling in the leaves of the adult rosettes, is instructive for comparison with *O. Lamarckiana* (Pl. 1. fig. 6). Pl. 1. fig. 13 and Pl. 2. fig. 14 again show clearly the three types of leaves which appear in the development of a rosette. These are photographs of the *same* plant, taken with an interval of 8 days. Fig. 16 also exhibits the three leaf types. It must be said that photographs are frequently rather inadequate to represent the differences between related forms to those unfamiliar with the characters, yet it is hoped that a careful comparison of figs. 5 and 17, of 6 and 18, of 8 and 19, will give a true conception of some of the main differences between *O. Lamarckiana* and *O. laevifolia*. The stem-leaves of the latter are more or less furrow-shaped, and stand out stiffly from the stem. For a systematic enumeration of the characters, reference may be made to DeVries (1909, i. p. 309) or Gates (1909 *c*).

Pl. 2. fig. 20 shows the fruiting stage of a typical individual. Comparison with Pl. 3. fig. 31 for *O. rubricalyx* shows that the bracts are much narrower and shorter than in that form. Incidentally it may be observed in fig. 20 that late in the season the stigma sometimes pushes out of the bud and expands before the latter opens. As is well-known, the flowers of all the Oenotheras decrease rapidly in size towards the end of the season. But the decrease is not always in the same proportion in all parts of the flower. When the diminution in length of petals and sepals is more rapid than in length of style, the stigma will protrude from the unopened bud. This is not an uncommon condition in all the large-flowered Oenotheras late in the flowering period, and it of course increases the probability of crossing. But flowers which develop so late in the season have a very poor chance of maturing seed, and it is not believed that such a phenomenon has any adaptive significance in securing occasional cross-fertilization in the race. Crosses with other individuals are secured, in the large-flowered Oenotheras in America, through the visits of moths in the evening when the flowers open. The fact that part of the species composing the *Onagra* group are strictly self-pollinating while part are open-pollinated,

and that, on the whole, the former species, such as *O. biennis* and *O. muricata*, are more successful and widespread than the latter, such as *O. grandiflora* and *O. Hookeri*, does not favour the view that occasional crossing is a necessity or even an advantage in this genus.

Schouten (1908) in several cultures of *O. laevifolia* has found that it yielded various mutant forms, including *O. laevifolia salicifolia*, *O. scintillans*, *O. laevifolia nanella*, and *O. rubrinervis*.

O. brevistylis.

This form also was discovered by DeVries in Hilversum, but has never appeared in cultures of *O. Lamarckiana*. Its almost completely sterile ovaries render its propagation possible only by using its pollen to cross with another form, so that it must clearly have originated as a mutant, very probably in the locality where it was found. The characters of this form have not been accurately shown in previous accounts. Pl. 2. fig. 21 shows how distinct are the young seedlings from *O. Lamarckiana* (Pl. 1. fig. 1), *O. rubrinervis* (Pl. 2. fig. 25), or *O. laevifolia* (fig. 15), the blades being characteristically broader than in any except *O. Lamarckiana*, from which the leaves differ in having longer petioles and (at this time) very little crinkling. Pl. 2. fig. 22 is a characteristic mature rosette, showing some leaves broad-pointed, but many having obtuse, blunt tips such as never occur in the mature rosette of *O. Lamarckiana* (*cf.* Pl. 1. fig. 5). There is always this wide range of variation in the tips of the leaves of each rosette. This is shown in Pl. 2. fig. 23, with which Pl. 1. fig. 6 of *O. Lamarckiana* should be compared. It will be seen that the ranges of variability overlap, though *O. Lamarckiana* never bears a leaf with tip as blunt as the broadest *O. brevistylis*, and *O. brevistylis* never bears a leaf with tip as narrow as the narrowest *O. Lamarckiana*. Hence, again as in *O. laevifolia*, though their ranges of variation overlap there is no doubt whatever that these two forms are perfectly distinct. If there were any doubt regarding the distinctness of the rosette stage it could be set at rest when the plants mature, for not only has *O. brevistylis* sterile ovaries but its style is extremely short so that the stigma barely projects above the calyx-tube, and the free tips of the sepals are also very short, as shown by Pl. 2. fig. 24. In addition, the terminal rosettes of the branches are more compact than in *O. Lamarckiana*, the bracts being shorter, with broader and less pointed tips. I found no difficulty in identifying the rosettes of *O. brevistylis* when mixed with *O. Lamarckiana* and was able to confirm my determination in each case when the plants bloomed, by opening a bud and discovering the very short style. It would be impossible to obtain more conclusive proof that a range of variation which is apparently continuous is in reality not so, for in the ontogeny of one series of individuals we pass from the rosette stage which yields a continuous series of leaf-shapes and in which there is some difficulty in recognizing the two types, to the flowering stage in which all the flowers of each individual are recognizable at a glance as belonging to one type or the other. This race also furnishes a striking instance of what occurs in all these *Oenothera* forms, namely the "holding together" or correlated variability of characters affecting all parts of the plant, the rosette and stem-leaves as well as the flowers and fruits. One must adopt the

conception that some fundamental germinal change has occurred in the origin of *O. brevistylis*, presumably from *O. Lamarckiana*, that change exhibiting itself externally in a different response as regards leaf-shape, but also in the very short style and badly formed stigma, the short sepal tips, and the almost entire failure of the ovaries to mature.

DeVries was able to show that *O. brevistylis* will breed true when seeds were obtained by self-pollinating many flowers, but *O. brevistylis* has usually been propagated by using its pollen to cross with *O. Lamarckiana*, the offspring being about 50 per cent. *O. brevistylis* and 50 per cent. *O. Lamarckiana*. My cultures of *O. brevistylis* were from seeds of DeVries which had been grown in that way for five generations. The sixth generation in my garden yielded 92 plants, of which 55 were *O. Lamarckiana*, 34 *O. brevistylis* and 3 *O. lata* mutants. The seventh generation, grown last year, gave a similar result, showing that there is continued sharp alternative inheritance when this mutant is crossed with its putative parent; and there is no tendency for any of the leaf characters or flower characters to separate and be independently inherited in the F_2 or later generations. The logical conclusion is, therefore, that all these character-changes represent the external manifestations of one fundamental germinal change. The sterility of the ovaries serves to emphasize the depths to which the organism has been stirred. It appears that the changes have been so serious that the development of the ovaries is rendered almost impossible. It is possible, however, that the failure to produce seeds results, not from abortion of the ovules, but from the fact that pollen will not germinate on the imperfectly formed stigma.

O. rubrinervis and *O. rubricalyx*.

The mutant *O. rubrinervis* probably bears a somewhat different relation to its parent (*O. Lamarckiana*) from some of the other derivatives. DeVries (1907) has shown that when *O. Lamarckiana* or one of its mutants is used to pollinate *O. biennis*, Linn., two types are produced in the F_1, which he calls respectively *O. laeta* and *O. velutina*. This type of behaviour will be considered further in the section on hybridization, but it might be pointed out here that, as Honing (1911) has shown, *O. Lamarckiana* and *O. rubrinervis* differ from each other in characters which are analogous to the differences between *O. laeta* and *O. velutina*. In both cases the former has broader, the latter narrower leaves, the former has darker green leaves and the latter more long hairs, etc. I shall show later that *O. muricata*, Linn., from the wild condition also often produces a broad-leaved and a narrow-leaved type, so that this "double" condition is of fundamental interest in the hereditary behaviour of the genus, though its full meaning is not yet clear.

In my cultures of *O. rubrinervis* in 1907 a new form (*O. rubricalyx*) originated suddenly in a single individual. Its origin and subsequent behaviour when bred pure and in crossing have been described in a previous paper (Gates, 1911 *b*). It need only be said that this form is morphologically identical with *O. rubrinervis*, but differs strikingly in a physiological character—pigment-production; there being a large increase

in the amount of anthocyanin, particularly in the sepals, hypanthium and rosette-leaves. Photographs of *O. rubrinervis* and *O. rubricalyx* can, however, be used interchangeably, for the morphological characters are exactly the same in both. Pl. 2. fig. 25 shows a pan of seedlings of *O. rubricalyx* and *O. rubrinervis*, in which it will be seen that the leaves are narrower, more pointed and less crinkled than in *O. Lamarckiana* (Pl. 1. fig. 1). Fig. 26 represents an older rosette, in which the three types of rosette-leaves (*cf.* the rosettes of *O. Lamarckiana* and *O. lævifolia*) are present, though type 2 is inconspicuous in *O. rubrinervis*, differing from type 3 only in the more even margin, more rounded tip and less crinkling, but usually not having a broad blade sharply narrowed to the petiole. The rosette in Pl. 2. fig. 26 shows three leaves of type 1, and three of type 2.

There is considerable variation in the mature rosette of *O. rubrinervis* in width of leaf, amount of red developed in the midribs, amount of crinkling and pubescence, etc., so that certain individuals transgress the boundary line separating them from *O. Lamarckiana* in each of these characters or in several of them together. But the occasional indeterminable rosettes which occur nearly always show decisive characters when the plants come into bloom. The leaves of the mature rosettes also vary in the width of the leaf-tip, and Pl. 2. fig. 27 shows an individual with exceptionally broad tips. The transgressive variability between *O. Lamarckiana* and *O. rubrinervis* becomes more evident under varying or unfavourable conditions of growth. Thus in 1911, in a culture of *O. rubrinervis* × *O. Lamarckiana*, F_1, 64 rosettes developed, 12 of which were classed as *O. Lamarckiana* and 52 as *O. rubrinervis*. These were transplanted too late in the season to become annuals, so they continued to produce rosette-leaves. The leaves appearing towards the end of the season (September 27) on the *O. Lamarckiana* rosettes were much narrower and lighter green than normal, so that they were practically indistinguishable from *O. rubrinervis* leaves. It is evident that local conditions of nutrition have much to do with the fluctuating variability of the Oenotheras, often producing a surprising range of variation. But this is clearly distinct from the germinal variations, which are inherited in each generation.

Comparison of large numbers of rosettes of *O. rubrinervis* and *O. Lamarckiana* shows the impossibility of discriminating, merely by inspection, between fluctuating and germinal variations. Plants and animals frequently breed true to remarkably small differences, as many recent breeding experiments, particularly the work of Johannsen (1909) with "pure lines" in beans and of Jennings (1911) with *Paramecium*, show. The only way to determine whether the offspring of a variant individual will regress towards the mean of the race, or will reproduce its peculiarity in all or a portion of its offspring, is by growing its progeny and determining their characters.

Another example of the manner in which a plant may immediately react to a change of environment by producing new characters, is furnished by a large plant of *O. rubrinervis* which was removed from the garden to a greenhouse in September, 1907, while in flower. It continued to bloom, but the weight of the inflorescence soon bent the tall stem into a nearly horizontal position. Growth in this position continued and a series

of rosettes soon developed along the stem, each apparently from a transformed bra bud. One of these "lateral rosettes," which is evidently in part a response to a new gravitational stimulus, is shown in Pl. 3. fig. 28. These rosettes were very uniform, all having the same arrangement and shape of leaves. The latter were all of one type, which is very distinct from any of the leaves in the ordinary ontogeny of *O. rubrinervis*, or, for that matter, of any other form I know.

A flowering shoot of *O. rubrinervis* (this plant derived from *O. rubrinervis* × *O. Lamarckiana*) is represented in fig. 29 for comparison with *O. Lamarckiana* (Pl. 1. figs. 7 & 8). It will be seen that the stem-leaves of this individual are more crinkled than those of the *O. Lamarckiana* plant represented in fig. 8, though in general the leaves of *O. Lamarckiana* show this character more than those of *O. rubrinervis*. Honing (1911) believes that the *O. rubrinervis* from *O. rubrinervis* × *O. Lamarckiana* differs from pure *O. rubrinervis* and agrees with the *O. blanda* of Schouten (1908). But I have not been able to observe any constant difference between *O. rubrinervis* derived from this cross and *O. rubrinervis* of pure parentage.

Pl. 3. fig. 30 shows one of several tall plants of *O. rubricalyx* which were grown in heavy clay soil and, apparently as a result, developed no side branches. In this typical plant it will be seen that there is a gradual decrease in the amount of crinkling on the upper stem-leaves. Pl. 3. fig. 31 represents the fruiting stage of *O. rubricalyx*, showing the characters of bracts and capsules.

One other strikingly aberrant individual of *O. rubrinervis* which appeared in my cultures in 1911 must be briefly described. It occurred in a lot of 34 plants derived from the original *O. rubricalyx* mutant in the F_3, which probably represented a pure homozygous race of *O. rubricalyx*, for although all remained rosettes except the aberrant individual, yet 32 showed clearly the *O. rubricalyx* pigment character of the rosette. The aberrant plant, unlike the rest, scarcely developed any rosette but formed a tall stem. It resembled *O. rubrinervis* most closely, from which it differed in the following characters. The stem was smooth and terete, almost free from long hairs. The leaves were of harder texture, considerably thicker, broader (42 mm.), and more pointed than in *O. rubrinervis*. They were also stiffer, standing out from the stem, and some were furrow-shaped, but they did not resemble *O. laevifolia*. The flowers, which all showed the same peculiarities, had elongated squarish ovaries, hypanthium scarcely at all developed, bud-cone somewhat distorted, sepals with red stripes as in *O. rubrinervis*. The stamens were frequently more than 8 (one flower 10, another 13), crumpled and incompletely coalesced with the petals, which were very much reduced and pale cream colour. The stigma-lobes were variously distorted, and in several cases the pistil was composed of three separate styles united at the base, each style bearing only 3 stigma-lobes. In addition to these peculiarities, in six instances a leaf was formed in the axil of a bract, two of these leaves being "pitchers" or ascidia. In one case a "pitcher" and a normal leaf were both found in the axil of a single bract.

This peculiar plant formed no seeds, but was preserved as an herbarium specimen. Its flowers recalled in some respects the virescent flowers of a certain race of *Oenothera*

which I described several years ago (Gates, 1910 *c*), but were quite unlike them in other features. This is another case of a mutation which is unable to perpetuate itself, and its chief interest lies in showing how various are the germinal departures from the parent form which may take place.

The data regarding my cultures of *O. rubrinervis* and *O. rubricalyx* may now be summarized. In 1907 I grew a total of 1112 plants of *O. rubrinervis*, all but 82 of which were the purely fertilized offspring of a culture of *O. rubrinervis* plants, numbering 45, grown in the previous year, 15 of the latter being used as parents for the second generation. The *O. rubricalyx* mutant appeared in this lot. One *O. rubrinervis* mutant also appeared in 1907, in a culture of 170 plants of *O. Lamarckiana* from pedigree seed.

I shall not add anything to what is already published regarding *O. rubricalyx* (Gates, 1911 *b*), except to state that in 1911 I obtained a pure (homozygous) race, in which all the rosettes exhibited the red character on their ventral surfaces. Six other cultures of *O. rubricalyx* in the F_3 gave altogether 41 *O. rubricalyx* and 51 *O. rubrinervis*.

Regarding the nature of the change which led to the appearance of the *O. rubricalyx* mutant, it seems clear that the original mutant individual was heterozygous, and originated from a cross between a germ-cell in which the new dominant character appeared and one in which it was lacking. This is shown (1) by the fact that all the *rubricalyx* plants of the F_1 tested were heterozygous, and (2) that the F_1 from this plant contained in addition to the 11 *O. rubricalyx*, one *O. rubrinervis*. The latter must have originated from two germ-cells of the original mutant, both of which contained only the recessive *O. rubrinervis* character.

The germinal change in the germ-cell which united with a normal *O. rubrinervis* germ-cell to form this heterozygous mutant was, as I pointed out elsewhere (Gates, 1910 *b*), probably fundamentally quantitative—a difference in capacity for anthocyanin-production which manifests itself throughout the plant.

O. gigas.

As is now well-known, this mutant has 28 chromosomes, double the number present in *O. Lamarckiana* and most of the mutants. The structural changes which were correlated with this nuclear change have been investigated in previous papers (Gates, 1909 *d*, 1911 *c*) and need not be further considered here, except to recall that the tetraploid number of chromosomes is associated with a doubling in the volume of the nuclei and a very large increase—in varying proportions according to the tissue—in the size of the cells. It seems that the gigantic stature of *O. gigas* (which expresses itself in stoutness of parts rather than tallness) results directly from the larger size of its cells, and it is probable that the number of cells is approximately the same as in *O. Lamarckiana*. Several similar cases which confirm this result have since been discovered in other plants. Compare *Wikstroemia* (Strasburger, 1910), *Musa* (Tischler, 1910), Mosses (É. & É. Marchal, 1909 and 1911). In animals, however, at least in Echinoderm and

Crustacean larvæ, it appears from the results of Boveri (1905) and Artom (1911) that, although doubling in the number of chromosomes in the race is followed by corresponding increase in the volume of the nuclei and cells, yet a regulation in the *number* of cells takes place, so that the resulting larvæ are not of gigantic size. This appears at present as an interesting difference between plants and animals, there being apparently no marked diminution in the number of cells in certain at least of the tetraploid races of plants. It seems not improbable that this lack of regulation in cell number in plants may be due to the greater thickness and rigidity of the cell-walls in plant embryos and tissues, so that the controlling action of the young organism as a whole is not able to express itself in re-arranging the cells as formed, in such a way that fewer and larger cells will compose the growing embryo.

O. gigas also exhibits a wider range of variability in leaf-shape than any other of the mutants from *O. Lamarckiana*. Pl. 3. fig. 32 represents a typical rosette, but in a large culture the leaf-blades range from practically orbicular to narrowly linear. In each individual, however, all the leaves are usually of the same shape within narrow limits of fluctuation, though occasional rosettes show considerable variation in this regard; nor have I observed the same succession of ontogenetic stages of the rosette as in *O. Lamarckiana*, and the other forms already described, in the *O. gigas* from DeVries's cultures. So far as I have observed in this race of *O. gigas*, leaves corresponding to type (1) and type (2) in *O. Lamarckiana* and *O. laevifolia* do not occur, at least under ordinary conditions of culture. In 1909 I grew a culture of 434 plants of *O. gigas*, constituting the sixth generation from the original mutation of DeVries from *O. Lamarckiana*. Pl. 3. fig. 33 shows the range of variation in leaves taken from the mature rosettes. In each rosette all the leaves belonged to one type. Pl. 3. figs. 34, 35, 36 & 37 represent individual rosettes, the range of variation being astonishing. Schouten (1908) attempted to isolate six types from the series of forms, but states that the offspring of any one type showed the whole range of variation, so that this could not be done. On account of the strongly biennial character of *O. gigas* only four plants of my culture came into flower. From these I raised 48 plants in the following year, but the numbers were not large enough to test the inheritance of this remarkable range of variations. They indicated, however, that the offspring of each plant tended to resemble its parent, though occasional rosettes departed from this rule *.

In Pl. 3. fig. 38 the buds of *O. gigas* are shown, two-thirds natural size. As will be seen, they are very much larger than those of *O. lata* (Pl. 3. fig. 43, left), which they most resemble. Cytological examination showed that the particular individual whose buds are here represented possessed 28 chromosomes. This plant produced much pollen, which was used in making several crosses.

An interesting form which frequently appears in families of *O. gigas* is a dwarf, *O. gigas nanella*. It is photographed in Pl. 3. fig. 39 on the same scale as the previous rosettes, to show its comparative size. It has not the *O. nanella* leaf-shape, but is

* It is probable that the meiotic chromosome distributions are fundamentally concerned in the determination of these various types.

merely a dwarf or miniature *gigas* of the broad-leaved type. Different dwarf rosettes show much variability in leaf-shape, the dwarf character being the only thing they have in common. Schouten states that his plants of *O. gigas nanella* showed the same pathological conditions as his *O. nanella*, but I have found no indication of it in my cultures. It is evident that the dwarf character is directly due to an inherited germinal change in both cases.

The percentage of dwarfs in my cultures of *O. gigas* was large. Out of 339 plants, one lot contained 4·28 per cent., another lot 8·76 per cent., while a third lot of only fifteen plants contained 10·9 per cent. Schouten's (1908) cultures of *O. gigas* yielded in 1906 2·01 per cent. *O. gigas nanella*, or 24 plants in 1196; and in 1907, among about 1000 *gigas* plants, which were chiefly the offspring of selected individuals of the previous year, appeared a total of 1·87 per cent. dwarfs, one culture yielding as high as 14·81 per cent. The meaning of this behaviour is not yet clear.

All individuals of the *O. gigas* of DeVries's cultures are descended from one individual mutant. Nilsson (1909) reports obtaining another *O. gigas* mutant in a culture of 30 *O. Lamarckiana* which were the offspring of one individual *. In the following year this *O. gigas* individual yielded 8 plants, all having the characters of *O. gigas*.

In 1909 I obtained from the Botanical Garden at Palermo, Italy, a packet of seeds under the name *Oenothera cognata*. A portion of these seeds were sown in 1911, and yielded 56 rosettes. The young plants apparently belonged to a new and unknown race. Their leaves had very long petioles, and the blades were ovate with broad tips, gradually tapering to the petiole. Some of these leaves are shown in Pl. 3. fig. 40. They resemble type (1) in the younger rosettes of *O. Lamarckiana* or *O. laevifolia* as already described. As previously stated, I have never observed this type of leaf in cultures of DeVries's *gigas*. As the rosettes of *O. cognata* develop, however, there is a sudden transition to the *O. gigas* type of leaf, and the mature rosettes—after more of the second type have been produced and those of the first type have died away—are absolutely indistinguishable from *O. gigas*. Pl. 3. fig. 40 represents the transition stage, when both types of leaf are present. These plants were all biennials, and hence produced no seeds, but a fresh sowing has yielded a few plants, from which the characters will be more fully determined. The number of the chromosomes has not yet been examined †.

The mature rosettes of this culture exhibited the same variations as my cultures of *O. gigas*, though the extremes of variation were not observed. Three dwarf rosettes, corresponding to *O. gigas nanella*, also occurred.

Enquiry at the Botanical Garden at Palermo elicited the information that the race had been derived in cultivation, apparently being descended from a single individual mutant. They have since lost the strain. It is evident, then, that this was an independent mutation, and it remains to be seen whether the race differs constantly from *O. gigas* in its earlier ontogenetic stages, for the mature rosettes are identical with that form. From this and other data, some of which will be referred to in this paper, it is

* See also Nilsson (1912) for further data.

† The chromosome number for typical plants has since been found to be 28.

evident that the Oenotheras cultivated in Botanical Gardens have for years been exhibiting phenomena of mutation closely similar to or identical with those studied by DeVries in his garden. Certain of these new forms, such as *O. cognata*, have been noticed by gardeners, given names, and made the basis of new local races. Their origin is just as sudden and discontinuous in Botanical Gardens as in experimental plots, and is therefore clearly not due to continued selection. Each race appears, at once, full-fledged, the descendant of a single aberrant individual.

O. nanella.

I have grown hundreds of plants of *O. nanella*, and while they exhibited a wide range of leaf-form, yet they have never been found to give rise to mutants. *O. nanella* has never been known to throw any of the other mutants, and, in this respect, it differs from several of the other types. But in very large cultures, dwarfs having the characters of other mutants sometimes appear from *O. nanella*. Thus (Zeijlstra, 1911) 18,649 plants of *O. nanella* derived from a previous generation were without exception dwarfs, but three of them possessed *oblonga* and one *elliptica* characters. *O. nanella* itself differs from *O. Lamarckiana* not only in stature but in leaf and flower characters.

The rosettes of *O. nanella* in my cultures are more variable than those of any other mutant except *O. gigas*. These variations will not be illustrated here, but the buds are shown, two-thirds natural size, in Pl. 3. fig. 41, with a bract attached to one. The bud-cone is usually shorter and slenderer than in the other forms.

Dwarf or *nanella* forms of nearly all the mutants are now known, including *O. lata nanella*, *O. gigas nanella*, *O. nanella-oblonga*, *O. nanella-albida*, *O. nanella-elliptica*, and *O. nanella-scintillans*.

Regarding the nature and cause of the dwarf character of *O. nanella*, Schouten (1908) has suggested that it results from a pathological condition of the plant, due to bacterial action, and invokes Eriksson's mycoplasma theory to explain its hereditary transmission. He states that the rosettes of *O. nanella* become sickly and die back; but careful observation has revealed nothing of this nature in my cultures, which shows that the phenomenon he describes is due to some local condition. Zeijlstra (1911) has since found that a *Micrococcus* inhabits the cells of the stem in *O. nanella* in his cultures, which indicates its greater susceptibility than other forms. That different forms differ widely in their susceptibilities to fungal attacks, I have found to be true of other species of *Oenothera*. Zeijlstra believes that the peculiar leaf-characters and the very short internodes of *O. nanella* are a result of the parasite, because occasional side branches appear which are dwarf yet have *O. Lamarckiana* leaf-characters and longer internodes than the main stem. He therefore thinks that a dwarf *O. Lamarckiana* appears as the result of a mutation, but that the parasite which attacks the dwarfs distorts them and causes their development into the "*O. nanella*" form. Whether a parasite really produces this effect can only be determined by infection experiments. Even if the hypothesis were true, it would remain unexplained why all the *nanellas* which appear are affected. I have obtained several dwarf races, having quite unlike

characters, in cultures of 75 races related to *O. grandiflora*, so that evidently the dwarfing of *O. nanella* is not primarily due to a parasite, although the presence of bacteria may make it smaller than it otherwise would be.

In the case of *O. gigas*, I have shown (1909 *d*) that the larger size of the plant is fundamentally concerned with the larger size of the cells and their nuclei, which in turn is connected in a causal relation with the doubled number of chromosomes. Preliminary measurements of cell-size in *O. nanella*, by a student, indicate that they are considerably smaller than the corresponding cells in *O. Lamarckiana*. I expect to investigate the question of cell-size in *O. nanella* more fully, but in the meantime it is very probable that the small stature of *O. nanella* may be at least partially explained on the basis of the cell-size, the dwarfness being a character of the cell. The many other changes in the shape of leaves, etc., are probably, like those of *O. gigas*, not so simply explained (*cf.* Gates, 1909 *d*, 1911 *c*). It seems evident, in any case, that the dwarfness of *O. nanella* is a cell problem (although the number of chromosomes remains 14) and is not produced by any pathological condition induced by other organisms.

Gauchéry (1899) (and other papers might be cited) classes dwarfing as of two kinds, (1) constitutional nanism, (2) induced nanism. From an anatomical examination of a number of dwarfs, he concludes that the reduction in the number of elements in the stem, and in their calibre, is very variable according to the tissue considered. Thus, the dimensions of the xylem vessels are always reduced, but this is not always true of the dimensions of the other cells; and in one case there is even shown an increase in the size of the cortical cells, though in all the other elements of the stem there is a decrease in size. The reduction in the dimensions of the epidermal cells was found to be much less than in the vessels.

O. lata and *O. semilata.*

The mutant *O. lata* has occurred a number of times in my cultures, as shown in the following table:—

TABLE III.

Culture.	Number of plants.	Number of *O. lata*.	
O. rubrinervis	96	1	
O. Lamarckiana × *O. brevistylis* ..	92	3	
O. Lamarckiana.....	117	2	
O. rubrinervis × *O. nanella*	42	1	
O. rubrinervis × *O. Lamarckiana* (from *O. lata* × *O. Lamarckiana*).	64	1	
Total	411	8	= 1·95 per cent.

Pl. 3. fig. 42 shows a typical rosette. The very characteristic buds are shown in

Pl. 3. fig. 43, reduced. The three buds to the left of the figure are *O. lata* buds as they appear in plants derived from seeds of DeVries. These flowers produce practically no pollen. An account of the pollen development in this form was published in 1907. The phenomena of sterility are very similar to those occurring in hybrids, as Tischler (1908) has also pointed out. The pollen mother-cells or young pollen-grains break down in various stages of development. The tapetal cells disappear early, and the wall-cells of the anther grow into the cavity of the loculus, more or less completely filling it with tissue. This ingrowth of the surrounding cells is doubtless due to the release of pressure on their surfaces caused by the disintegration of the tapetal cells and the pollen mother-cells. In some cases it is evident that mitoses of the ingrowing cells have also taken place. The sterility is, therefore, not due to the ingrowth of the tapetal cells, but the pollen mother-cells themselves frequently begin disintegration, from some unknown cause at an earlier stage of development.

The *O. lata* derived from the Amsterdam cultures, wherever it is grown, is almost or quite completely sterile in its anthers. This sterility is closely correlated with the shape of the bud. As the illustration (Pl. 3. fig. 43, three buds to the left) shows, the buds are thick and clumsy, rounded, not squarish, radially asymmetrical, exhibiting a characteristic protrusion, swelling or hernia on one side of the cone near the top. This is in turn due to the crumpling of the petals and their distorted disposition in the bud. It is evident that this irregularity in the development of the petals is closely associated with the failure of pollen development.

Whatever causes the sterility of the pollen is also concerned in the distortion of the petals, and therefore of the buds, in this characteristic manner. That this is the case is clearly shown by the behaviour of a pollen-producing form of *O. lata*, which is one of many types occurring in a culture of naturalized Oenotheras from Birkenhead, near Liverpool, an account of which occurs elsewhere in this paper. This form is probably to be classed as *O. lata*, though it differs slightly from H. DeVries's mutant in the characters of the rosette (see Pl. 4. fig. 44), the leaf-blades being somewhat less crinkled, more elongated and with longer petioles than in typical *O. lata*, though the ranges of variability of the two forms appear to overlap in these respects. The individual represented in fig. 42 probably agrees most nearly with DeVries's *O. semilata*. But the majority of these rosettes agreed more nearly with *O. lata*. The flowers, however, were fertile, producing considerable quantities of good pollen, and its buds have nearly or quite the normal squarish shape of other pollen-producing mutants, as shown by the four buds to the right in Pl. 3. fig. 43, although there remain some traces of the crumpling of the petals seen in typical *O. lata*. Whether these plants should be classified as *O. semilata* or as a polleu-producing race of *O. lata* is difficult to decide, on account of the variability. MacDougal (1907, p. 15) first mentioned a successful self-pollination of this Liverpool form, supposing it to be an exceptional condition. My 1909 culture of 107 plants from one lot of seeds from Birkenhead contained 8 *O. lata* individuals with the bud-characters just mentioned, all of which produced considerable quantities of pollen, and two others whose place is somewhat doubtful, as they never

fully developed. One plant of this culture, however, corresponded in all respects with the *O. lata* of DeVries, having the characteristically distorted buds and sterile anthers.

It is now clear that *lata* possesses 15 chromosomes in some at least, and probably in all individuals. The presence of the extra chromosome is probably the cause of the failure in the pollen development. The varying distributions of the odd chromosome in the megaspores, and perhaps also partial apogamy, probably account for the inconstancy of the offspring from this mutant. The chromosome-number of *semilata* is not yet known, and the problem regarding the relation between the extra chromosome and the *lata* characters therefore remains to be solved.

If one thinks of the *lata* characters as emerging from those of *O. Lamarckiana*, and the *semilata* characters as only half emerged, one gets a picture of the relationships of these three forms.

O. semilata is one of the rarest of the mutants, having appeared only three times in DeVries's cultures, and every time from *O. lata*. One such mutant self-fertilized gave 358 plants, all of which were *semilata* except three which were *nanella* and four *lata*. In a cross, *O. lata* × *O. semilata* gave 105 plants distributed as follows:—61 *Lamarckiana*, 39 *lata*, 2 *nanella*, 2 *oblonga*, 1 *albida*, which is similar to the result obtained when other forms are used to pollinate *O. lata*.

I obtained four plants showing the characters of *O. semilata* in a culture of 75 plants from *O. lata* × *O. Lamarckiana*. The offspring were as follows:—63 *O. Lamarckiana*, 4 *O. lata*, 2 *O. lata nanella* (?), 2 *O. semilata*, 1 *O. laevifolia* (?), and 3 aberrant rosettes, 2 of which were probably *O. semilata*. The kaleidoscopic fluctuations of these plants during their ontogeny often renders their determination a matter of great difficulty. The F_2 from one of these self-fertilized *O. semilata* plants produced 40 very variable rosettes. About 11 of them were *O. semilata*, but the rest formed a continuous series running to *O. Lamarckiana* and could not be more accurately determined. Three which came into bloom were all clearly *O. semilata*. The other *O. semilata* plant produced in F_2 only three plants, all of which were *O. Lamarckiana*.

O. semilata is only known as a mutant from *O. lata*, unlike most of the other mutants which have appeared from various ancestors. As DeVries has stated, its external characters suggest that it is an intermediate hybrid between *O. lata* and *O. Lamarckiana*, and the fact that its offspring breed true does not exclude this interpretation. The fact that *O. semilata* has only occurred from the single source, *O. lata* × *O. Lamarckiana*, supports the view that it is such an intermediate hybrid, rather than a mutant, but its chromosome number may explain why it originates only from *O. lata*.

My castration experiments with *O. lata* (1909 *b*) have furnished an indication that some form of apogamy occasionally, though rarely, occurs in this mutant. It seems possible that perhaps 1 per cent. of the ovules will develop seeds without fertilization, though the remaining ovules require fertilization for their development.

The characters of the other mutants from *O. Lamarckiana*, which have been less thoroughly studied, will not be discussed here. The data presented in this section are

meant to give a better understanding of the differences between the more common mutants and their parent form, as well as their relationships to each other. It is clear that the mutants differ from each other not in one but in many characters, and I am in agreement with the conception of DeVries that all these characters are in each case the expression of a single germinal change.

But the appearance of so many so-called "combination types," particularly in the cultures of Schouten (1908), shows that all the characters do not necessarily remain together under all circumstances. The "combination types" are supposed to originate from the union of two germ-cells which have mutated in different directions, but the significance and manner of origin of such types, and their relation to hybrid splitting, will have to be determined by future investigations. If *O. nanella*, for instance, is capable of producing occasional types in its offspring such as *O. nanella-oblonga*, *O. nanella-elliptica*, *O. n.-lata*, and *O. n.-scintillans*, then each of these leaf-types must be potential or "latent" in *O. nanella* just as they are in *O. Lamarckiana*, and the only quality really absent from *O. nanella* is stature. But "latent" is a dangerous word to use, for it is only a cloak for ignorance regarding the real cause. It is possible, though not probable, that some of the mutants from *O. Lamarckiana* appear only as alternative dichogenous conditions which are environmentally determined very early in the ontogeny. On the other hand, certain of them may be present in some germinal condition resembling the heterozygous condition in Mendelian hybrids. But this question and others relating to the interpretation of the mutation process are discussed in another section.

O. grandiflora, Solander.

The previous paragraphs dealt with *O. Lamarckiana* and its derivatives. A later section will consider the derivatives from a naturalized colony of forms on the sand-dunes of Lancashire which included both *O. Lamarckiana* and *O. grandiflora*. The latter species has already been carefully described (Vail, 1907) from plants derived from the locality in Tensaw, Alabama, where it still survives. It is frequently grown in Botanical Gardens, and, particularly in France, it often goes under the name *O. suaveolens*, Desf. I have grown cultures from the *O. grandiflora* naturalized in Lancashire, and also from plants collected in the original locality in Alabama by Prof. S. M. Tracy. I have already pointed out that this species formerly had a wide range in America, extending eastwards to the Atlantic, where it long survived in Virginia and Carolina. The eastern form probably differed in certain features from the Alabama form.

In July, 1907, I began a greenhouse culture from seeds collected wild on the Lancashire coast, for which I was indebted to Dr. D. T. MacDougal. The rosettes were transplanted to individual pots when quite young, and they developed slowly and perfectly under these conditions. About half of them were proved by their striking rosette characters, and afterwards by their flowers, to belong to *O. grandiflora*. Pl. 4. fig. 45 shows one of these rosettes four months after germination, and Pl. 4. fig. 46 the same type at the age of five and a half months. In the latter figure a new leaf-type has appeared, with characteristic basal lobes, though the old type of leaf remains. This is

the most striking case I have observed, of change in leaf-characters during the ontogeny of a rosette. Pl. 4. fig. 47 shows the adult rosette of the same type at the age of nine months, the rosettes having been kept constantly under tropical conditions, so that they developed slowly and displayed their characters to the full. In fig. 47 the characteristic type of leaf with pinnatifid basal lobes continues to be produced, and the first type has disappeared. In the *O. grandiflora* type of rosette ontogeny there are, then, three leaf-types as in *O. Lamarckiana* and some of its derivatives, but only types (2) and (3) are represented in figs. 45 and 46. Type (2) in *O. grandiflora* is represented by a number of leaves, while in *O. Lamarckiana* and its relatives types (1) and (2) are only represented (at least in out-of-door cultures) by three leaves each. The number of leaves of each type is probably always variable, depending upon the conditions of development.

When *O. grandiflora* is grown under ordinary cultural conditions—*i. e.*, when the seeds are sown in January and the young plants are planted out in May or June—the adult type of rosette-leaf with pinnatifid lobes is usually omitted entirely; and frequently, as I shall show in other *O. grandiflora* races, there is no rosette at all, the young plant forming a stem with internodes almost at the very beginning. This interesting difference from *O. Lamarckiana* in physiological behaviour results in the plants developing more rapidly, and frequently blooming earlier. Pl. 4. fig. 48 shows such a plant of typical *O. grandiflora* in my cultures from Alabama. The absence of a rosette gives the plant a shrub-like appearance. Such plants were top-heavy, and it was necessary to have them staked in order to prevent their being broken down by the wind. Fig. 48 also shows the ovate-lanceolate shape of the stem-leaves in *O. grandiflora*. They taper at both ends, the lower end narrowing to a petiole, and (except the uppermost bracts) are not sessile with aurate base, as is usual in *O. Lamarckiana*. Such buds are shown, reduced in size, in Pl. 4. fig. 49. Unlike those of *O. Lamarckiana* and all its derivatives, the buds are free from long, muricated hairs, though they usually bear soft, pubescent hairs, but are sometimes quite glabrous. Fig. 49 also shows the range of red colour pattern in these buds.

O. biennis, Linn.

It is well-known that a large number of North American geographical races of *O. biennis* exist. New species, such as *O. strigosa* and *O. canovirens*, are published as segregates from time to time, but many others exist, and my experience in growing numerous races from wild seeds collected in various parts of the continent has been that usually each new locality yields a race which is recognizable as distinct by its leaf-characters and habit. One of the most interesting questions in connection with the evolution of the Oenotheras is, How have these races arisen and what relation do they bear to the evolution of the group? The fact that these forms are all self-pollinating adds to their interest and makes the question of their manner of origin and evolution somewhat different from that of the larger-flowered open-pollinated forms. For it is clear that in the latter intercrossing of races must frequently take place, so that the

evolutionary unit is here not a series of pure, self-fertilizing biotypes, but a population of interbreeding races whose constituency is changing within limits from generation to generation.

The two series of forms—open-pollinating and self-pollinating—are, however, not nearly so sharply separated as was formerly supposed. Later in the present paper I shall cite several cases in my cultures, of the appearance of small-flowered, short-styled, and hence self-pollinated plants from large-flowered, long-styled ones. I have even found several cases of transition from long-styled to short-styled flowers or *vice versa*, sufficient to cause the change from open-pollination to close-pollination, on the same plant. All such cases probably occur in hybrids between long-styled and short-styled forms. They are similar to the cases cited by Boulenger (1907). Since species are known having large flowers and short styles (*O. Simsiana* as well as *O. brevistylis*, in which the stigma is more or less rudimentary), and having small flowers with long style (*O. ornata*), it is evident that in the further light of the experimental evidence of transition referred to above, any sharp cleavage-line between open-pollinated and close-pollinated forms, such as was formerly thought to exist, disappears. Added evidence is furnished by the large-flowered, long-styled *O. grandiflora*, and its segregate, the small-flowered, short-styled *O. Tracyi*, which otherwise clearly resembles *O. grandiflora*. These grew together in Alabama and must have occasionally intercrossed.

I am growing the second generation of a number of distinct races of *O. biennis* from various sources. They differ chiefly in leaf-characters and will be described in detail at another time. The race of *O. biennis* which I have used in my hybrid crosses has already been described (MacDougal, 1905, p. 9), but I must add here certain photographs which are necessary for a comparison of the parents with the corresponding parts of their hybrid offspring. Pl. 4. fig. 50 represents a typical rosette of this race; Pl. 4. fig. 51, a flowering shoot; and Pl. 4. fig. 52, the same in fruit, to show the capsules and the size and other characters of the bracts. In Pl. 4. fig. 53 several buds are represented, reduced in size. Three of them, taken from different heights of the stem, show the great range of continuous variation in the size of bracts of an individual.

O. muricata, Linn.

This Linnean species has usually been distinguished from *O. biennis* by its smaller flowers and narrower leaves. But, as mentioned elsewhere (Gates, 1911 *d*, p. 580), I have found certain races having the flower-characters of *O. muricata* (*i. e.*, smaller than *biennis*), but with broad leaves. The narrower leaves of *O. muricata*, as a distinction from *O. biennis*, therefore breaks down and there alone remains the difference in size of flower.

The fact that *O. muricata* possesses both narrow-leaved and broad-leaved races, and that both frequently occur in the same locality and are probably derived from seeds of the same individual, is one of the most interesting discoveries in connection with my cultures of this group. For the broad- and narrow-leaved individuals differ in the same

general way as do *O. Lamarckiana* and *O. rubrinervis*. And more particularly, they differ in the same as do the "twin" types first described by DeVries, which are obtained in the F_1 when certain small-flowered forms, such as *O. biennis* and *O. muricata*, are pollinated from *O. Lamarckiana* or its derivatives. It, therefore, seems probable that this twin hybrid behaviour depends upon a double alternative (broad- or narrow-leaved) condition in the wild state. My cultures of *O. muricata* from such widely separated regions as Middleton, N.S., St. John, N.B., and Winnipeg, Manitoba, in Canada, have revealed in each case two distinct races, the two being respectively identical from all three localities. This shows not only the wide distribution of these particular types East and West on the continent (though probably confined to a narrow range of latitude), but since the two types were found in each case from a single collection of seeds, and since they occur in strictly self-pollinating forms having the flower-characters of *O. muricata*, it is evident that this twin behaviour can hardly be due to pollination from large-flowered forms. This is especially true since no large-flowered forms are known to occur in the regions where these seed collections were made, and they are certainly absent at least from the Nova Scotia region.

In short, then, we have to account for the occurrence of broad-leaved and narrow-leaved "twin" types in races which it is reasonably certain were purely self-pollinated. And the same behaviour was repeated in collections of seeds from three widely separated areas. All races of *O. muricata* do not show two types, however, several collections of seeds having yielded uniform races with only one very constant type.

The broad-leaved and narrow-leaved types from my collection of seeds from Winnipeg, are represented respectively in Pl. 4. figs. 54 and 55, while fig. 56 shows a plant of the broad-leaved race from Nova Scotia, in flower. Its rosette is identical with that of fig. 54. I have as yet been unable to test the behaviour of the twin races, except to show that the broad-leaved type breeds true. Seeds of *O. muricata* sent to me from the Bremen Botanical Garden were found also to contain two types which differed but slightly if at all from the plants from the three localities in Canada already mentioned. The total numbers of broad- and narrow-leaved individuals from these four sources were respectively 30 and 27, indicating possibly a tendency to appear in equal numbers. It must also be said that the two types were very distinct, as represented in the photographs, without any tendency to be obscured by variation.

Another lot of seeds, received from the Kiel Botanical Garden under the name *O. biennis*, yielded 37 plants belonging to two very distinct types: type (1) (26 plants) had very broad, large, light-green rosette-leaves; type (2) (11 plants) had narrow, dark-green leaves with long unmargined petioles. These two types were both unlike the previously mentioned "twin" types, and were so unlike that it seems probable they may have been thrown together by an accidental mixing of seeds.

On the other hand, I have collected seeds near Woods Hole, Mass., which yielded a single uniform race of *O. muricata*, apparently corresponding with the var. *canescens* of Robinson, and remaining true in the F_2. Seeds kindly sent by Mr. E. L. Rand, from near the beach at Seal Harbour, Maine, also yielded a single, uniform race with

characteristic narrow, dark-green leaves often having red midribs. A young seedling is shown in Pl. 5. fig. 57, and a nearly mature rosette in fig. 58. The young seedlings are very characteristic, forming tiny, compact rosettes of dark-green leaves closely hugging the ground. The number of leaves in the young seedlings seems to increase much more rapidly than in *O. biennis*, *O. grandiflora*, or *O. Lamarckiana* forms, though I have not determined the reason for this. The young plantlets also have a stouter, harder (usually reddish) stem, and their roots are longer, making it more difficult to pull them from the ground. All these differences are perhaps adaptations to a more rigorous environment. Another collection of wild (naturalized) seeds from near Berlin, sent through the kindness of Professor E. Baur, yielded a uniform race apparently identical with the last. In a culture of *O. ammophila* from the Bremen Botanical Garden I was unable to find any constant distinction from certain races of *O. muricata*.

It is perhaps worth noting that in all cases where one uniform race was derived from a collection, it was always a narrow-leaved type. Another interesting fact which shows the extreme closeness between the organism and its environment, and the way in which a slight environmental difference will induce a whole race of *Oenothera* to modify markedly its development, is shown in my cultures, already mentioned, of *O. muricata* var. *canescens*. In 1910 this race was grown in a very wet, rich soil, with much humus, and the whole race (69 plants) without exception formed very imperfect rosettes and then shot up slender, unbranched stems. The offspring from this race were grown the following year in a much drier, poorer soil, without fertilizer, and with little humus. These plants (22) again reacted uniformly in producing rather large rosettes, and, finally, forming shoots with many long basal branches, giving them a pyramidal appearance. The leaf and flower characters were, however, unchanged. Similar facts are, of course, a matter of common knowledge to all who grow plants, but the numerous and varied responses of which the plant is capable under varying environment are often neglected or insufficiently considered, both in systematic descriptions and in experiments on heredity.

My studies of *O. muricata* from collections of seeds thus far renders it probable that the individual races are less numerous and more wide-ranging than is the case with *O. biennis*. It also seems probable that the *O. muricata* forms are, on the whole, distinctly more northern in distribution than *O. biennis*, there being possibly a relation between smaller flower-size and higher latitude or altitude, though at present this is not clear, for apparent exceptions occur. In any case, it could only be true in a very general way.

The following table summarizes my cultures of *O. muricata* races. Several other cultures were unfortunately killed. The detailed description of these races will be considered at another time.

TABLE IV.—*Races of* O. muricata, *Linn.*

Culture.	Number of Plants.	Broad-leaved.	Narrow-leaved.	Remarks.
O. muricata, Linn., Winnipeg, Man.	11	4	7	The races from Winnipeg and Middleton are identical, and that from St. John is at least *very* closely similar.
,, ,, Another sowing ..	2	0	2	
,, St. John, N.B.	10	3	7	
,, ,, Another sowing ..	4	0	4	
,, Middleton, N.S.	8	5	3	
,, ,, Second sowing....	5	2	3	
,, ,, Broad-leaved, F_2 ..	33	33	0	Two plants of the F_1 with broad leaves gave only broad in F_2.
,, ,, ,, F_2 ..	21	21	0	
,, Bremen Botanical Garden	17	16	1	Apparently identical with the Winnipeg races.
"*O. biennis*, Linn.," Kiel Botanical Garden.....	37	11	26	Both races different from Bremen culture.
O. muricata, Linn., Berlin (naturalized)	148	..	148	Uniform race.
,, Seal Harbour, Maine	186	..	186	Uniform, same as Berlin race.
,, var. *canescens*, Robinson, Woods Hole, Mass...	69	..	69	Uniform race.
,, ,, ,, F_2..	29	..	29	,, ,,

V. (A) CULTURES OF OENOTHERAS FROM LANCASHIRE.

These cultures, which were begun in July, 1907, have developed so many features of interest that a separate account of them is necessary. We may recall that these Oenotheras have been occupying the Lancashire sand-dunes for at least a century, and probably date from a much earlier time. It is, therefore, of much importance to know what has been happening to this complex of forms during the period of its naturalization. An inquiry regarding the process of evolution in such a genus as *Oenothera* must continually keep in mind a freely-intercrossing population as its starting-point, and as the condition under which its evolution has gone forward. An analysis of the changes which the plants may show as a result of freely commingling for a long period is, therefore, of great importance, especially in its bearing on the relation between crossing and the phenomena of mutation.

Bailey (1907) first called attention to the fact that *O. Lamarckiana* was growing on the sand-dunes at St. Anne's-on-Sea, and MacDougal (1907, p. 8) found that seeds from

this locality produced *O. Lamarckiana* and several of its mutants, including *O. lata*, *O. rubrinervis*, *O. oblonga*, and *O. albida*. My cultures from near Birkenhead have shown that *O. grandiflora* is an equally conspicuous member of the *Oenothera* population of that locality. *O. grandiflora* and *O. Lamarckiana* have also intercrossed freely, producing a complex of forms which I have since succeeded in part in analyzing. The latter frequently display characters, particularly of the leaves, which are entirely different from anything known in *O. Lamarckiana* or its mutants, though the bud and flower characters usually correspond with *O. Lamarckiana* (as do the mutants of DeVries) or are intermediate between *O. Lamarckiana* and *O. grandiflora*. This fact provided the first clue to the relationships of these aberrant types. I have isolated a number of these types, which are now being grown in the second or third generation. They will be described at a later time. These cultures are, therefore, an attempted analysis of a typical interbreeding colony of forms. It is hoped that naturalized or indigenous colonies of Oenotheras in other parts of the world will be subjected to a similar analysis, for it is only by this means that any full knowledge of the factors at work in the evolution of the genus can be gained. I shall be grateful for seeds sent to me from any locality.

The question which must be asked regarding the Lancashire Oenotheras is, Are all these new aberrant races the direct result of hybrid combinations, or must an additional factor of mutation be invoked to account for the origin of some of them? We have already seen that, in the case of the mutants from *O. Lamarckiana*, such a factor *must* be invoked, for the origin of certain of the mutant characters cannot be explained on the basis of hybrid splitting. In the case of the Lancashire Oenotheras, it is evident that many of the new races at least are complex hybrids, even although they breed true. Whether any of them have had a different origin, remains to be seen. In any case, the mutational process (using the term in contradistinction to hybrid splitting) is probably a result of the germinal disturbance which the race has experienced through previous crossing. On this view, mutation and hybridization are closely related processes, the former being an indirect result of the latter. This does not exclude the possibility, indeed probability, that mutational transformations may result also from environmental action on the organism, or from other causes.

We may now consider some of the results of an experimental analysis of these forms—an analysis which is not yet completed, but certain results of which need to be stated. It will be remembered that these forms are in part derivatives from *O. Lamarckiana* and in part complex hybrids between *O. Lamarckiana* and *O. grandiflora* races. It is possible that *O. biennis* may also have entered into their composition, though I have no direct evidence of this.

My first culture of these forms consisted of 56 plants grown in a tropical hothouse (see Gates, 1912). Half of these developed the characteristic *O. grandiflora* rosette (see Pl. 4. fig. 47), while the remainder displayed a large number of curious rosette types, scarcely two being alike, but all falling in the series of *O. Lamarckiana* and its mutants, clearly rather widely divergent from *O. grandiflora*. The rosettes developed their characters to the fullest extent, and seven of these (Pl. 5. figs. 59–65) are selected to

show the range of types represented *. The other rosettes approximated more or less to these, though no two were quite identical. The variability, both of this and an independent outdoor culture the following year, was far greater than DeVries's race of *O. Lamarckiana* exhibits. Fig. 59 represents a rosette (No. 5) belonging to the *O. lata* race already described (p. 36) as originating from this locality. Its leaves differ constantly from the *O. lata* of DeVries (*cf.* Pl. 3. fig. 42). Pl. 4. fig. 44 shows another rosette of this *O. lata* race as grown in outdoor culture. The greater elongation of the blades and petioles is the feature distinguishing both from the race of DeVries. The buds of the two have already been contrasted (Pl. 3. fig. 43). The individual (No. 5) represented in Pl. 5. fig. 59 produced a somewhat fasciated stem with straggling, irregular branches, probably a result of the tropical environment. Its rosette closely resembled No. 6, which was elsewhere described (Gates, 1912, pl. 2) as continuing to form rosette-leaves without internodes. No. 5 was self-pollinated, and its F_1 grown out-of-doors in the usual way yielded the following interesting series of types. Three of the offspring produced rosettes like their parent, *i. e.* they were *lata*-like, but the flowers were as small as in *O. biennis* and the anthers surrounded the stigma in the bud. The buds bore numerous muricated hairs, and the bud-cones were somewhat barrel-shaped (type 1). To the next type belonged 7 plants, a very distinct type represented in Pl. 5. fig. 66, having very narrow, almost elliptical, whitish leaves of uniform width (type 2). This rosette agrees with DeVries's *O. elliptica* (*cf.* 'Mutation Theory,' i. 394, fig. 83), but the flowers were small with the anthers surrounding the stigma. Two other plants (type 3) resembled most those just mentioned, but were dwarfs. Four plants belonged to another type (Pl. 5. fig. 67) having small flowers in which the anthers were almost or quite touching the base of the stigma-lobes (type 4). This unexpected appearance of short-styled flowers would indicate an ancestral cross with *O. biennis*. I have, however, never discovered *O. biennis* in my cultures, numbering several hundred plants, from this locality. Of course, there remains the possibility that the tropical conditions under which the fertilization and development of the seeds of the mother plant took place may have served to call forth "latent" characters in the race, which it had acquired through previous crossing.

However, I grew outdoors an independent culture from a second sowing of Lancashire seeds, and these revealed (among many types) one constant type with flowers intermediate between *O. biennis* and *O. Lamarckiana*, so this furnishes very good evidence that *O. biennis* has, at a previous time at any rate, formed a part of this colony. The behaviour of three races which belonged to *O. grandiflora*, though differing somewhat among themselves, may be summarized here. One race (54×32) was typical rather broad-leaved *O. grandiflora*, agreeing closely with the Alabama form. The F_1 contained 11 plants and the F_2 82 plants which bred perfectly true. Another race (No. 40), the F_1 from one plant, contained 43 individuals. This race also belonged to *O. grandiflora*, though differing in minor points from the last, and it was much less uniform. Several plants omitted the rosette stage and 5 were dwarfs. One of the dwarfs produced in the

* It will be observed that in hothouse cultures the number of rosette-leaves is always greater than out-of-doors.

F_2 a uniform race numbering 23 plants. They varied in height from one to two feet, but otherwise agreed in having *O. grandiflora* flowers and general leaf characters. This dwarf race of *O. grandiflora* is clearly different from *O. nanella*. Still another dwarf race had the following history. It arose in another race (No. 49) which closely resembled No. 40, the plant yielding in F_1 80 offspring which were fairly uniform, except one rosette which resembled an overgrown *O. gigas*, and 2 dwarfs. The next generation from one of the latter yielded a uniform progeny of 20 plants. Unlike the last dwarf races, they averaged only one foot high, and their leaves resembled *O. nanella*, but they had *O. grandiflora* flowers and buds. It is evident, then, that constitutional dwarf races may easily occur in these forms.

Numerous other types are now being grown in F_2 and will be described in detail later. My cultures of these forms furnish abundant evidence that rather uniform true-breeding races can be obtained from this evidently hybrid progeny. Indeed, my experience has been that most of these races of hybrid ancestry will breed reasonably true, at least, after the F_1, though, as might be expected, there is usually more variability in these races than in the mutants of DeVries which have been inbred for a number of generations.

In all cases of which I am aware, of crosses between large-flowered and small-flowered Oenotheras (see Section on hybridization, p. 52), the flowers of the F_1 hybrids are intermediate, both as regards size of petal and length of style. As showing that an analysis of a mixture of races such as I am describing is possible, I may refer to one race (070.4) derived from a single individual in my sowings of 1908. The first generation of offspring from this plant numbered 60 uniform individuals, and four of these, self-pollinated, yielded in all over 200 for the second generation. They constituted a very uniform race, and a careful comparison showed that their characters were identical in every respect with those of the hybrid *O. nanella* × *O. biennis*, which also breeds true (*cf.* Section on hybridization where the rosettes are described). The stem-leaves of this race (070.4) were found to be rather exceptionally variable, varying from pointed at both ends and petiolate, to sessile with broad base, uncrinkled. The dimensions of the flowers were as follows:—length of ovary 8 mm., hypanthium 32 mm., cone 29 mm., sepal tips 5–8 mm., diameter of cone at base 5–7 mm. There is considerable variability in the length of style, the stigma being above the anthers in some, but touched by their tops in others, though it is apparently never so long as in *O. Lamarckiana* or so short as in *O. biennis*. This race much resembles *O. rubrinervis* in general appearance, on account of its usually red midribs in the rosette-leaves. But the buds are shorter and more slender (base of cone 9 mm. in diameter), the rosette-leaves are usually less crinkled, and the two forms cannot really be confused, the smaller flowers, of course, making the race distinct.

The numerous other races I am now cultivating from this source will be described in detail elsewhere. Abundant confirmation is, however, already furnished for the interesting fact that in *Oenothera* hybrid races with characters intermediate between their parents frequently breed true. The question of the gametic composition of such races, and the reasons why they breed true, will be referred to in the next section.

These cultures also by showing that, in addition to *O. grandiflora*, *O. Lamarckiana*, and its mutants as known from DeVries's experiments, a host of other forms occur in a freely interbreeding population, raise the question as to the origin of the latter forms, and the limits and relations between hybridization and mutation. The first step in answering that question is taken by isolating the many races and learning their characters. The next step is to recombine them in various ways and determine the results of those recombinations or by independent syntheses to build up hybrid races having the same characters. By such means we may expect ultimately to understand the relation between hybridization and mutation phenomena.

Finally, it is important to note certain facts regarding the history of this colony of Oenotheras. It must perhaps always remain uncertain whether the *O. Lamarckiana* in this colony was transported as such from the other side of the Atlantic, or whether it originated in the colony as a result of crossing. I have pointed out that in the latter case it would have had an equal chance of originating in the region of Virginia, where both *O. biennis* and *O. grandiflora*, the only forms which could have given rise to it, were formerly wild. In any case, the important fact, from an evolutionary point of view, is that *O. Lamarckiana* and its derivatives, such as *O. rubrinervis*, are now the dominant feature of this *Oenothera* colony. Whether or not they have originated in that colony, they are the forms which will provide most of its future population, and, therefore, determine any future evolution it may undergo. If *O. Lamarckiana* has originated there as a hybrid, then it has largely overcome its parent species in the struggle for existence, and its descendants will be the survivors for the next evolutionary step.

(B) Cultures from Botanical Gardens.

I have obtained seeds of various *Oenothera* species from nearly all the Botanical Gardens in Europe. A number of these cultures have contained distinct surprises. I have already mentioned certain ones in other connections, but a few more will be added here. Of course, the names under which seeds are received cannot always be relied upon. I have received *O. Lamarckiana* several times under the names *O. biennis* or *O. biennis grandiflora*. For instance, seeds from the Botanical Garden at Kolosvar, Hungary, under the name *O. biennis grandiflora* were found to be nearer *O. Lamarckiana* than any other species, though not typical of its mean condition. Again, seeds from the same garden under the name *O. erythrosepala*, Barb., developed *O. Lamarckiana* and one typical *O. lata* mutant.

A lot of seeds of *O. suaveolens*, Desf. (= *O. grandiflora*), from Nantes Botanical Garden yielded nearly 200 plants, which showed a great range of variability with every evidence of previous crossing. Many of the rosettes closely resembled *O. Lamarckiana*, while some were very similar to *O. rubrinervis*. Among other aberrant types, there were one dwarf and two with short styles. The flower dimensions in one of the latter were as follows: ovary 15–17 mm., hypanthium 47–51 mm., petals 40–42 mm. long. The style, however, was very short so that the stigma was below the anthers. The sepals were reddish, and the plant somewhat resembled a *brevistylis* form of *O. rubrinervis*. All

the flowers on this plant were alike, with very little variation. These flowers would not be self-fertilized in the bud because the style was too short. In the other short-styled individual the styles were somewhat longer, so that in the first flowers the stigma was just below the anthers, and in later flowers was touched by the anthers, as in *O. biennis*. I have not yet determined whether these two aberrant plants resulted from germinal or fluctuational variation, probably the former.

VI. Hybridization in *Oenothera*.

In this section will be taken up (1) various experiments in crossing the mutants with each other and with *O. Lamarckiana*, and (2) the results of crossing various forms with *O. biennis*. The race of *O. biennis* used in these crosses came from New York State, and has already been described by MacDougal (1905, p. 9). Its main features are here illustrated in Pl. 4. figs. 50–53.

The results of these crossing experiments partly confirm DeVries's experiences in crossing *Oenothera* forms, though there are certain contradictory results. An effort has been made—particularly in the description of the hybrids between *O. biennis* and other forms, where it is most needed on account of the brevity of DeVries's descriptions of the twin hybrids—to make the description and illustration of the various forms, and their relation to each other and to their parents, as clear as possible. The complete description and accurate comparison of these hybrids, not merely in taxonomic language, but so as to bring out the relationship of their characters, is a difficult task, but one which is essential to an elucidation of the laws of inheritance in these forms.

After the hybrids have been described, and the results of crosses compared with those of DeVries, an attempt will be made to give a résumé of the various types of inheritance now known to occur in *Oenothera*. This seems particularly necessary because the results of *Oenothera* crosses have received little attention in the recent literature of hybridization. In the last section I showed that races of *Oenothera* which are of hybrid origin frequently breed true, and this is in entire accord with the results of crossing-experiments. From a survey of all the hereditary phenomena in the genus, it appears that there are two general types of behaviour: (1) alternative inheritance; (2) blended inheritance. How far these may represent fundamentally different processes will be discussed after the data are presented.

(a) *Crosses involving* O. Lamarckiana *and its Mutants.*

DeVries made a number of crosses between *O. Lamarckiana* and its mutants, with the result that both parental forms appeared in the F_1, and both usually bred true in later generations. I have made similar crosses, with results which corroborate those of DeVries. The data from some of these crosses may now be stated.

O. lata × *O. Lamarckiana* yielded in 1906 five *O. lata* and eight *O. Lamarckiana*. Six of the latter, self-pollinated, produced a total of 104 plants in 1907, all of which were *O. Lamarckiana*, showing no difference whatever from *O. Lamarckiana* of pure

parentage. Again, *O. rubrinervis* × *O. Lamarckiana* (the latter derived from a cross with *O. lata*) gave in one case (No. 115 × 77) 32 *O. rubrinervis*, 5 *O. Lamarckiana*, and 1 which was uncertain. In another case (No. 121 × 78), with parents of the same ancestry, the result was 49 *O. rubrinervis*, 16 *O. Lamarckiana*, and 1 *O. lata*. In one case, from *O. rubrinervis* × *O. Lamarckiana*, the F_2 from a *rubrinervis* plant of the F_1 gave 82 individuals exclusively *O. rubrinervis*, and a *Lamarckiana* plant from the F_1 of the same cross yielded 19 plants purely *O. Lamarckiana*, bearing out DeVries's result that splitting in the F_2 does not occur. The data from these and three other crosses are brought together in the following table:—

Table V.

Date.	Cross.	Number of Plants.	Offspring.
1906.	*O. lata* × *O. Lamarckiana*, F_1	13	*O. lata* 5 + *O. Lamarckiana* 8.
	O. Lamarckiana, F_2 (6 plants) ..	104	*O. Lamarckiana* 104.
1906.	*O. rubrinervis* × *O. Lamarckiana*, F_1 ..	38	*O. rubrinervis* 32 + *O. Lamarckiana* 5 + 1 uncertain.
1906.	*O. rubrinervis* × *O. Lamarckiana*, F_1 ..	66	„ 49 + „ 16 + *O. lata* 1.
1907.	*O. rubrinervis*, F_2 (1 plant)	82	*O. rubrinervis* 82.
1907.	*O. Lamarckiana*, F_2 „	19	*O. Lamarckiana* 19.
1909.	*O. Lamarckiana* × *O. rubrinervis*, F_1 ..	68	*O. Lamarckiana* 22 + *O. rubrinervis* 45 + 1 mutant.
1910.	*O. Lamarckiana* × *O. rubricalyx*, F_1 ..	11	*O. Lamarckiana* 2 + *O. rubrinervis* and *O. rubricalyx* 8 + 1 mutant.
1910.	*O. rubricalyx* × *O. Lamarckiana*, F_1 ..	4	*O. Lamarckiana* 1 + *O. rubricalyx* 3 (rosettes only).
1909.	*O. Lamarckiana* × *O. gigas*, F_1	40	*O. Lamarckiana* 40.
1911.	„ × „ F_2 (2 plants)	44	*O. Lamarckiana* 44.
1907.	*O. rubrinervis* × *O. nanella*, F_1	42	*O. Lamarckiana* 20 + *O. rubrinervis* 20 + *O. lata* 1.
1907.	*O. rubrinervis* × *O. nanella*, F_1	3	*O. Lamarckiana* 1 + *O. rubrinervis* 2.
1907.	*O. lata* × *O. rubrinervis*, F_1	1	*O. oblonga* mutant.
1907.	„ × „ F_1	4	*O. Lamarckiana* 3 + *O. lata* 1. The *O. Lamarckiana* remained true in F_2 and F_3.
1910.	*O. rubrinervis* × *O. nanella*, F_1	79	*O. Lamarckiana* 25 (?) + *O. rubrinervis* 52 + 2 aberrant.
1910.	*O. rubricalyx* × *O. nanella*, F_1	42	*O. Lamarckiana* 7 + *O. rubricalyx* 35.

Though the numbers involved were small in several of these cases, yet the results are sufficient as confirmatory evidence.

In the cross *O. Lamarckiana* × *O. rubricalyx*, the *Lamarckiana* was from the F_2 of *O. Lamarckiana* × *O. gigas*. Its characters differed in no respects from *O. Lamarckiana* of pure ancestry, and its guarded offspring also bred true. Its behaviour was, therefore, in every way the same as that of pure *O. Lamarckiana*.

Again, when two mutants from *O. Lamarckiana* are crossed, *O. Lamarckiana* in addition to one or both of the parent types is usually obtained in the F_1. Thus, the cross *O. rubrinervis* × *O. nanella* was made by DeVries four times, and in each case the F_1 showed only two types, *O. Lamarckiana* and *O. rubrinervis*, the percentage of the latter varying from 92 per cent. to 25 per cent. And in the one case in which later generations of the cross were grown, the *O. rubrinervis* of the F_1 gave five types: (1) *O. Lamarckiana*, which proved constant; (2) *O. rubrinervis*, which also bred true; (3) *O. nanella*, whose constancy was not tested; (4) an intermediate type, *O. nanella rubrinervis*, which bred true; and (5) *O. rubrinervis*, which in the F_3 split again in the same manner into *O. Lamarckiana*, *O. rubrinervis*, and *O. nanella rubrinervis* (see DeVries, Die Mutationstheorie, ii. p. 451). The constant intermediate type, *O. rubrinervis nanella*, is virtually a much dwarfed *O. rubrinervis*. The foliage is that of *O. rubrinervis* but the leaves are smaller. The amount of dwarfing is not so great as in *O. nanella*, but it brings the plants much nearer the size of *O. nanella* than of *O. rubrinervis*.

The crosses made between mutants also show that *O. Lamarckiana* as well as one of the parent types appears in the F_1. *O. nanella*, however, is apparently an exception as it rarely or never appears in the F_1, the dwarf characters being recessive. These results are grouped together in the second part of Table V.

The sharp way in which the young seedling types are contrasted with each other is clearly shown in Pl. 5. fig. 68. This pan contains the F_1 from *O. lata* × *O. nanella*. Four of the seedlings (large and broad-leaved) are *O. Lamarckiana*, two *O. rubrinervis*, one *O. lata* (with crowded, broad, somewhat crinkled leaves and short petioles), one (small) uncertain, and one new mutant having narrow, elongated, whitish leaves with very little chlorophyll. The latter soon died from lack of nourishment.

(b) *Crosses with* O. gigas.

The results derived from crosses between the mutant *O. gigas* and other forms have been somewhat conflicting, but I think all can now be brought under one viewpoint without involving a contradiction. In the first place, *O. gigas*, when crossed with *O. Lamarckiana*, clearly differs from the other mutants in its behaviour, at least in certain cases. DeVries first showed that *O. gigas* × *O. Lamarckiana* and its reciprocal give an identical, uniform hybrid type, intermediate between the parents. He has since (1908) brought together the results of his crosses with this mutant, which may be summarized in the following table:—

Table VI.

O. gigas × *O. Lamarckiana*, F_1	62 plants.	F_2 224. A constant, intermediate race.
O. Lamarckiana × *O. gigas*, F_1	969 „	F_2 180. Same as reciprocal.
O. gigas × *O. brevistylis*, F_1	..	.. Same as above.
O. gigas × *O. rubrinervis*, F_1	17 „	„ „
O. rubrinervis × *O. gigas*, F_1	236 „	„ „
O. lata × *O. gigas*, F_1	133 „	68 intermediate between *O. lata* & *O. gigas*. 65 „ „ *O. Lamarck.* & *O. gigas*.
O. biennis × *O. gigas*, F_1	84 „	Intermediate type.
O. gigas × *O. biennis*, F_1	66 „	„ „
O. muricata × *O. gigas*, F_1	66 „	„ „
O. gigas × *O. muricata*, F_1	34 „	„ „

To these may be added the results of Miss Lutz (1909), who from *O. lata* × *O. gigas* obtained an F_1 of 40 plants, containing three types: (1) *O. lata* (two plants, each having 15 chromosomes); (2) *O. gigas* (six plants, each having about 30 chromosomes); (3) a more or less intermediate and variable group of 32 plants, having also an intermediate number of chromosomes—22, 23, or 21.

In similar crosses, Geerts (1911) reports the following results from counting the chromosomes of *O. gigas* hybrids: *O. lata* × *O. gigas* gave an F_1 containing a *lata*-like type and a *gigas*-like type, both having 21 chromosomes. This is contrary to the results of Miss Lutz, though he omits to quote the latter. *O. gigas* × *O. Lamarckiana* and its reciprocal gave a constant intermediate type, though the F_1 contained 21 chromosomes and the F_2 are said to contain only 14. That is, though the number of chromosomes changes from 21 to 14, there is said to be no change whatever in the external characters. In the light of the results of Miss Lutz above quoted, this may well be doubted. Further, I have shown (Gates, 1909*d*) that *O. gigas* has conspicuously larger cells in its various tissues, a fact which is undoubtedly closely connected with its larger dimensions. It is, therefore, highly improbable that the nuclei and cells, and hence various dimensional characters, of the F_2 are identical with those of the F_1. Indeed, Geerts's own figures, in the paper referred to, prove that the nuclei, and doubtless also the cells, are smaller where the chromosome number is smaller, as I had shown previously.

I made the cross *O. Lamarckiana* × *O. gigas* in 1909, and obtained an F_1 of 40 plants the following year. They were all identical with *O. Lamarckiana* in every respect, and several which were examined contained only 14 chromosomes. Two of these plants yielded an F_2 of 44 plants which were indistinguishable from *O. Lamarckiana*. Of course, there is the possibility that an error may have occurred, in collecting the wrong capsule from the original mother plant, but all such errors are guarded against as carefully as possible.

These facts are paralleled by a recent result of Miss Digby (1912) with *Primula*. It was found that *P. floribunda* var. *isabellina* × *P. kewensis* gave an F_1 resembling the seed parent. The former parent has 9 chromosomes as x number, while the latter has 18 as x number, yet the F_1 contained only 18 chromosomes as $2x$ number. It seems probable that the extra 9 are extruded in the divisions of the embryo.

In view of the results of Miss Lutz, in which two *O. lata* plants having 15 chromosomes occurred in the F_1 of a cross with *O. gigas*, and the result of Geerts's that the chromosome number in these crosses is 21 in F_1 and becomes 14 in F_2, we may assume that an extrusion of the extra chromosomes from the nuclei has occurred, in some cases during the division of the fertilized egg in the original cross, in other cases during the reduction divisions in the F_1 plants. The former case would be in harmony with certain results of Baltzer, Herbst, and Tennant in connection with the behaviour of the chromosomes in hybrid Echinoderm larvæ, in which the extrusion of certain chromosomes takes place during cleavage.

This leaves unexplained the result of Miss Lutz in obtaining six pure *O. gigas* plants having the *gigas* chromosome number, in the F_1 of *O. lata* × *O. gigas*. There is another possible explanation of the two *lata* plants in the F_1 of this cross, namely, that they originated apogamously. I obtained experimental results some time ago (Gates, 1909 *b*) which showed with a certain degree of probability that a small percentage of the ovules of *O. lata* will develop without fertilization.

It is clear that further experiments are required before these somewhat conflicting results can be fully understood. It is at least evident, however, that *O. gigas* differs from the other mutants in giving, in some cases, an F_1 which is intermediate between the parents, in other cases two or three different types; and it appears that the variation in crossing-behaviour is closely connected with the distribution and fate of the chromosomes in the various hybrids.

(c) *Crosses between* O. biennis *and* O. Lamarckiana *and its derivatives.*

These crosses between large-flowered and small-flowered forms display a number of interesting and peculiar features. (1) The reciprocal crosses are not alike, the hybrids being usually distinctly patroclinous. (2) These hybrid races breed true in later generations, except in certain characters such as dwarfing, in which they split. (3) Certain crosses (chiefly those in which *O. Lamarckiana* or one of its derivatives is the pollen parent) exhibit two types in the F_1, both of which are different from either parent. These DeVries calls twin hybrids. They are respectively broad- and narrow-leaved, and are called *laeta* and *velutina*. The same *laeta* and *velutina* types may be derived from several different crosses, or they may differ in certain minor characters according to the parents used. (4) The flowers of these hybrids appear to be in all cases intermediate in character between those of the parents. The flowers are larger than *O. biennis*, but smaller than *O. Lamarckiana*, and the styles are short enough so that the anthers touch the base of the stigma and secure self-fertilization. There is, however, a considerable range of variability in both these features of the hybrid flower.

DeVries has described this type of hybrid behaviour in several papers (1907, 1908, 1909), and Andrews (1910) has added anatomical notes on the structure of the hybrids, but no figures of these hybrids have been published. In a number of crosses which are summarized in Table VII. (p. 56), I have obtained results which are in general agreement with those of DeVries, though certain probably important differences are to be

noted. The numbers of plants are, unfortunately, often small on account of sterility, the biennial habit, etc.

In regard to all these crosses, it must be said that fluctuating variability frequently obscures the results and renders the formation of sharp categories very difficult. The characters of these hybrids, such as broad and narrow leaves, are particularly responsive to slight differences in nutrition, such differences producing in some cases great variation in the width of leaves in one type, in other cases obscuring the line between two different types. Apparently the best conditions for displaying the *laeta* and *velutina* characters are, in a rather poor soil, with very little fertilizer but plenty of water. The types then appear very sharply distinct, not only in width of leaf, but in colour, pubescence, and crinkling. Owing to this obscuring fluctuation and to environmental influences, I am still uncertain whether *O. Lamarckiana* × *O. biennis* and *O. nanella* × *O. biennis* yield a single fluctuating type or two types which are distinguished only by width of leaf. The two crosses with *O. rubricalyx* given in the table are merely additional to those already published (Gates, 1911 *b*), in which it was shown that *O. rubricalyx* behaved the same as its parent *O. rubrinervis*.

The two sharply distinct rosette types derived from *O. biennis* × *O. Lamarckiana* are shown in Pl. 5. figs. 69 & 70, which represent *laeta* and *velutina* respectively. That *O. biennis* × *O. laevifolia* yield two types which are, in some crosses, identical with the preceding, is shown by Pl. 6. figs. 71 & 72. The rosettes from this cross sometimes show much variability, however, and I have obtained rosettes which were exactly intermediate between *O. biennis* and *O. laevifolia*, as shown in Pl. 6. fig. 73 (*cf.* Pl. 4. fig. 50 and Pl. 2. fig. 17). The basal jagged teeth of this hybrid are such as frequently occur in *O. biennis*. Flowering shoots of the narrow- and broad-leaved hybrids derived from *O. biennis* × *O. Lamarckiana* are shown in Pl. 6. figs. 74 & 75, where the difference in width of stem-leaves is clearly seen. Other differences between these types, as regards flowers, etc., have been described by Andrews (1910).

As the twin types mature, their characters gradually converge, so that in the fruiting stage they are wholly indistinguishable. This is due to the rapid diminution in length and width of the bracts of both types. In Pl. 6. fig. 76 are shown, two-thirds natural size, several buds of the *velutina* type from *O. biennis* × *O. Lamarckiana*, in which the bracts pass from relatively broad and as long as the flower-bud, to very narrow and less than half the length of the bud. The characteristic hairiness of this type of bud is also seen in the photograph (*cf.* Pl. 3. fig. 41 for *O. nanella* and Pl. 4. fig. 53 for *O. biennis*). A fruiting shoot of *O. biennis* × *O. laevifolia* is shown in Pl. 6. fig. 77. The twin types are at this time wholly indistinguishable from each other and from the two types in *O. biennis* × *O. Lamarckiana*. The measurements of the buds in *O. biennis* × *O. laevifolia* were as follows: ovary 11 mm., hypanthium 28 mm., bud-cone 20 mm., sepal tips 9 mm., petals 30 mm. maximum, usually less.

The results derived from the reciprocal crosses are not quite so clear on account of the obscuring effect of fluctuation, but in a general way there appears to be one rather widely fluctuating type. Its broader-leaved varieties (which are the most frequent) are very

similar to the broad-leaved type derived from the reciprocal cross, as will be seen by comparing Pl. 6. fig. 78 with Pl. 5. fig. 69. But a narrower-leaved type frequently appears and breeds fairly true in later generations. This type has identical characters in *O. Lamarckiana* × *O. biennis* and in *O. nanella* × *O. biennis*. A typical rosette is shown in Pl. 6. fig. 79. It is markedly narrower-leaved than fig. 78, and comes true to its difference, yet it does not resemble the *velutina* or narrow-leaved type derived from the reciprocal cross (*cf.* Pl. 6. fig. 79 with figs. 70 & 72). Whether, therefore, with *O. biennis* as the pollen-parent we derive two types differing only in leaf-width (and not in other characters, as do *laeta* and *velutina*), or whether this represents a single type with widely fluctuating variability, I am not prepared to decide. Another cross, *O. nanella* × *O. biennis*, yielded a large offspring with a continuous range of variation in leaf-width, but agreement in other characters. If there are two types in this cross they differ from each other, then, only in leaf-width, and not, like *laeta* and *velutina*, in a series of other foliage characters.

Another point with regard to these hybrids, *O. nanella* × *O. biennis*, *O. Lamarckiana* × *O. biennis*, and (*O. nanella* × *O. biennis*) × (*O. Lamarckiana* × *O. biennis*), which are all identical, is that some of the young seedlings are frequently lacking somewhat in chlorophyll, giving them a whitish appearance. These individuals form smaller rosettes with yellowish centre, but otherwise agree with the type. These rosettes finally, however, "catch up" to the others, and the appearance of two distinct types in the seedlings is seen to be due to the presence of weaker individuals which contain less chlorophyll and hence grow more slowly. I have not determined whether this constitutional weakness is inherited. A fruiting shoot of *O. Lamarckiana* × *O. biennis* is shown in Pl. 6. fig. 80, for comparison with fig. 77 and Pl. 4. fig. 52.

That the reciprocal hybrids differ from each other, even at an early age, is evident from a comparison of Pl. 6. figs. 81 & 82, which represent respectively *O. biennis* × *O. nanella* and its reciprocal. Comparison with fig. 83, which represents pure *O. nanella* seedlings, shows that both hybrid types differ from *O. nanella* even at this stage. It also shows that *O. biennis* × *O. nanella* is at this time patroclinous, most resembling *O. nanella*, while the reciprocal, with its long leaves and petioles, is nearer *O. biennis*.

As shown by the table (VII.), in *O. nanella* × *O. biennis*, and also in its reciprocal, I have obtained dwarfs in the F_1. This is contrary to the results of DeVries, who found the dwarf character recessive in the F_1, reappearing in the F_2. Thus (DeVries, 1908) in *O. muricata* × *O. nanella*, the F_1 gave *laeta* and *velutina*, about 50 per cent. of each, and the *laeta* type continued to breed true while the *velutina* split in the F_2 and later generations, giving about 60 per cent. dwarf *velutina* (*murinella*) and the remainder normal tall *velutina*. In the paper above referred to, DeVries concludes that *laeta* breeds true because its pollen carries only tallness, which is dominant over its own heterozygous egg-cells (tall and dwarf) but recessive to pure "dwarf" cells. The latter, however, is contradictory to the fact that in *velutina* tallness is dominant to dwarfness, and also leaves unexplained why *laeta* does not split while *velutina* does split. Further experiments will be required before this contradiction can be cleared up.

Another result which has not previously been recorded is as follows: The *velutina* from the F_1 of *O. biennis* × *O. Lamarckiana* was pollinated by *O. Lamarckiana*, giving the three types *laeta*, *velutina*, and *O. Lamarckiana*. This cross when repeated gave the same result, the proportionate numbers being, moreover, about the same in both cases—*i. e.*, the *velutina* were five or six times as numerous as the other types, though the numbers were rather small for determining ratios (see Table VII.). It was hoped that a number of other crosses which I had made would permit a solution of this interesting situation, but many of them failed to develop, so the results are still incomplete.

With the above should be compared the two cases (Table VII., p. 56) in which the hybrid *O. Lamarckiana* × *O. biennis* was pollinated by *O. Lamarckiana* and yielded a series of rosettes which apparently contained the two types *O. laeta* and *O. Lamarckiana*, though there is much variability. A further series of crosses will be necessary before this behaviour can be fully understood. According to DeVries (1911) (*O. Lamarckiana* × *biennis*) × *Lamarckiana* gives pure *Lamarckiana* at least as regards rosette characters, for he does not speak specifically of the flowers. It seems questionable whether the latter will not remain intermediate in all these hybrids. If the rosettes from this cross all belong to *O. Lamarckiana* they show, at least in my cultures, a much greater range of fluctuation than pure cultures of that form yield.

In the important paper above referred to, DeVries describes double reciprocal hybrids between *O. biennis* and *O. muricata*, the results being in agreement with the predictions, on theoretical grounds, of Giglio-Tos (1908, 1911). Thus (*O. biennis* × *muricata*) × (*muricata* × *biennis*) gives *O. biennis* which remains true, and (*O. muricata* × *biennis*) × (*biennis* × *muricata*) gives *O. muricata*.

(d) *Results.*

It would at first appear, from a survey of all the results of crossing in the genus *Oenothera*, that we are dealing with four distinct types of hybrid behaviour: (1) crosses of *O. Lamarckiana* with its mutants, except *O. gigas*; (2) crosses of *O. gigas* with various forms; (3) crosses between the large-flowered and small-flowered species of *Oenothera*; and (4) Mendelian behaviour in occasional characters such as in *O. brevistylis* and *O. rubricalyx* when crossed with their parents. But I believe it can be shown that types (1) and (3) are essentially the same, and the peculiarities of type (2) in which it differs from the behaviour of the other mutants are, as I have already indicated, probably to be explained in connection with the presence of a double set or tetraploid number of chromosomes, the members of the extra set of chromosomes varying in their distribution in different hybrid crosses.

In the first place, it is possible that the appearance, for example, of *O. rubrinervis* and *O. Lamarckiana* in the F_1 of crosses between these forms is only an extreme case corresponding to the *laeta* and *velutina* appearing in, e. g., *O. biennis* × *O. Lamarckiana*. In both cases, later generations of both types breed true (usually), the difference being that in the former case the types derived from the cross are at least closely similar to, if not identical with, their parents, while *laeta* and *velutina* are quite as different from

Table VII.

Date.	Cross.	Number of Plants.	Offspring.
1908.	*O. Lamarckiana* × *O. biennis*, F_1	9	Uniform intermediate type.
1909.	„ × „ F_1	40	Type I., 37 plants, same as *O. nanella* × *O. biennis.* „ II., 3 plants, broad-leaved.
1909.	„ × „ F_2	1	*O. oblonga* rosette.
1910.	„ × „ F_2	3	1 *Lamarckiana* rosette. 1 *velutina* rosette. 1 small rosette *Lamarckiana* (?).
1911.	„ × „ F_2	2	Small rosettes, apparently *oblonga*.
1911.	(*O. Lamarckiana* × *O. biennis*, F_2) × *Lamarckiana*	9	7 rosettes, most like *Lamarckiana.* 2 „ like *laeta.* All may belong to one type.
1911.	(„ × F_2) × *Lamarckiana*	13	4 „ *Lamarckiana.* 8 „ „ or *laeta.* 1 *oblonga*, smaller flowers.
1911.	*O. rubricalyx* × *O. biennis*, F_1	20	Uniform type.
1909.	*O. biennis* × *O. Lamarckiana*, F_1	39	24 *velutina.* 14 broader-leaved (*laeta*). 1 very close *O. biennis.*
1909.	„ × „ F_1	4	2 narrow-leaved (*velutina*). 2 broad-leaved (*laeta*).
1910.	„ × „ *laeta*, F_2	21	All *laeta*, flowers intermediate.
1910.	„ × „ *velutina*, F_2	51	All *velutina*, one dwarf rosette.
1910.	(*O. biennis* × *O. Lamarckiana*) *velutina* × *O. Lamarckiana*	40	30 *velutina* rosettes. 4 *laeta* rosettes. 5 *Lamarckiana* rosettes. 1 mutant rosette.
1911.	(*O. biennis* × *O. Lamarckiana*) *velutina*, F_2	2	2 *velutina.*
1911.	(„ × „) *velutina* × *O. Lamarckiana*	14	10 *velutina* rosettes. 2 *laeta* rosettes. 2 *Lamarckiana* rosettes.
1909.	*O. biennis* × *O. lævifolia*, F_1	4	2 *velutina*, same as in *O. biennis* × *O. Lamarckiana.* 2 *laeta*, „ „ „ „
1910.	(„ × „) *velutina*, F_2	12	12 *velutina.*
1911.	(„ × „) *laeta*, F_2	18	17 *laeta.* 1 *velutina*, flowers intermediate.
1910.	*O. biennis* × *O. rubricalyx*, F_1	34	*laeta* and *velutina*, much variation.
1908.	*O. nanella* × *O. biennis*, F_1	7	One type, same as *O. Lamarckiana* × *O. biennis.*
1910.	„ × „ F_1	9	„ „ same as last.
1909.	„ × „ F_2	5	„ „ „ „
1910.	„ × „ F_3	13	„ „ same as last generation.
1910.	„ × „ F_1	62	60 *laeta*, broad-leaved, somewhat variable type. 1 *velutina* (?), narrow-leaved rosette. 1 dwarf, with *O. biennis* flowers.
1911.	(*O. nanella* × *O. biennis* F_2) × (*O. Lamarckiana* × *O. biennis* F_1), F_1	16	One type, same as *O. nanella* × *O. biennis.*
1911.	*O. nanella* × *O. biennis*, F_3	13	„ „ breeding true.
1910.	*O. biennis* × *O. nanella*, F_1	43	28 *velutina.* 7 *laeta.* 6 dwarfs. 2 aberrants.

their parents as the latter are from each other, and the flowers remain intermediate. However, there is the difference that (*O. rubrinervis* × *Lamarckiana*) × (*Lamarckiana* × *rubrinervis*) presumably gives both *O. rubrinervis* and *O. Lamarckiana*, while (*O. Lamarckiana* × *biennis*) × (*biennis* × *Lamarckiana*) gives, if the result of DeVries is invariable (1911, p. 100), only *O. Lamarckiana*. But, as already stated, there is some reason to doubt the constancy of the latter result.

I have already expressed my agreement with Honing that *O. Lamarckiana* and *O. rubrinervis* differ from each other in the same way that the *laeta* and *velutina* hybrids differ—*i. e.*, in width of leaves, crinkling, hairiness, etc. This point has now been adequately proved by the careful studies of Honing. But, I have further shown in the present paper (p. 40) that *O. muricata* in the wild condition also frequently contains two types which differ from each other in similar ways. The appearance of both (twin) types in the F_1 of many crosses is probably a result of this dimorphic condition, which is therefore a fundamental one in this section of the genus. It remains for further studies to disclose the nature of the relation between the two types as regards origin, but it seems not impossible that they represent alternative conditions, either of which may come into expression under certain circumstances.

Certain results of Miss Saunders with Stocks (1908) and Petunias (1910) also indicate that races may breed true and yet be heterozygous, and it is probable that this is the explanation of the behaviour in such crosses as *O. rubrinervis* × *O. Lamarckiana*, although that is not yet proven.

From one point of view, especially regarding the origin of new characters, one of the most important features of heredity in *Oenothera* is that both blended and sharply alternative inheritance occur. The cases in *Oenothera* of blends which breed true in specific crosses are now well established. My cultures of Lancashire Oenotheras have also yielded several true-breeding races whose characters are evidently a blend of previously existing races. Certain crosses between these and other forms give the impression of an absolute blending of characters between races in the F_1. The behaviour of later generations of these hybrids is not yet known. It remains to determine whether, with repeated crossing back, blending continues to occur until the differences are obliterated. The reason for intermediate or blended races breeding true is not yet explained, but from the behaviour of certain of the *laeta* and *velutina* types (DeVries, 1908) it is possible that the failure of segregation may here also be due to a difference between the characters borne by the male and female germ-cells. On the other hand, it is not improbable that there is in such cases a real blend without segregation of the materials representing the germinal characters. It seems probable that when real blends occur, they will be found chiefly in characters which have a quantitative basis, yet certain apparent cases of this kind, such as *O. rubricalyx*, show sharp segregation phenomena.

Through the maze of these complicated types of behaviour, it is beginning to appear evident that there are certain connections between the systematic relationships of a form and its hereditary behaviour, and crossing therefore is one of the most fundamental

methods of analyzing those relationships. It is clear that forms which originate from the same parent do not all have the same hereditary behaviour towards that parent. Hence the relationship of their characters to the parent form is different in different cases, and, therefore, the change implied in their method of origin has been different. The hereditary behaviour of the mutants of *Oenothera* is also usually different from that of the related wild species. It seems justifiable to conclude that not only in Mendelian, but in other types of hereditary behaviour, the method or type of inheritance is determined in large measure by the nature of the characters themselves.

Our knowledge of heredity in *Oenothera*, therefore, shows that several types of inheritance exist, having an evident connection with the systematic relationships of the forms, or, in other words, with the nature of the differentiating characters of those forms. Blending and segregating inheritance both occur in *Oenothera*, and it is not yet clear in how far the former may be explained in terms of the latter.

VII. General Considerations and Summary.

From the foregoing pages it will appear that the explanation of the mutation phenomena in *Oenothera Lamarckiana* is by no means simple, and a full understanding of the nature and cause of this behaviour has not yet been reached. A number of facts, however, lead to the belief that the previous crossing which *O. Lamarckiana* has undergone, either in the wild condition or in Botanical Gardens, or both, has been the chief cause of the germinal disturbances which make themselves manifest in the appearance of mutants. The exact nature of these disturbances is not at present clear. Cytological studies, as well as the hereditary behaviour, show that the various mutational changes are of fundamentally different kinds, involving germinal alterations which are not only diverse among themselves but even appear in some cases to originate at different points in the life cycle. Thus, in *O. gigas* the essential change appears to have taken place in the megaspore mother-cell or in the early divisions of the fertilized egg, and possibly also during the reduction divisions in the pollen mother-cell; while the hereditary behaviour of the original *O. rubricalyx* mutant indicates that it was the result of a cross between a mutated and a non-mutated germ-cell. On the other hand, it is not easy to explain the behaviour of such mutants as *O. rubrinervis* and *O. nanella* on the theory of their hybrid or heterozygous origin, without involving a contradiction. *O. rubricalyx* gives in each generation a certain percentage of reversions to the parent form, *O. rubrinervis*, until a homozygous race is obtained, but in most of the other mutants no reversions occur.

It seems entirely probable, as DeVries believes, that the cause of the mutations is an internal one; and yet it cannot at present be decided whether this is due, for instance, to irregularities in chromosome distributions or to the action of slight releasing stimuli. In any case, the capacity for producing aberrant types is a result of germinal instability probably occasioned by previous crossing, the phenomena accompanying meiosis in the mutants resembling those found in hybrids in various particulars. It is evident that any explanation of mutation must take into account the peculiar chromosome behaviour in this group.

It by no means follows, however, that mutations appear only after a mixture of germ-plasms, and it is necessary to distinguish two types of mutations: (1) those following an ancestral mixture of germ-plasms, and (2) those occurring in pure lines.

The numerous and rapidly-accumulating cases of mutations, not only in *Oenothera* but in many other genera of plants and animals, make it impossible to ignore this factor as a method of species-formation, whatever its evolutionary significance may be. But series of chance-wise mutations could scarcely result in the orderly phylogenics we often see in the palæontological record; nor are they adequate to account for the more complex cases of adaptation, especially those involving inter-relationships between various organisms, though they may be capable of explaining cases of "climatic adaptation" in various species of a genus.

Darwin, in his theory of natural selection, also usually assumed a change in the climatic or biological environment of a species, which led ultimately to its modification. But the effects of climatic and distributional vicissitudes in the earth's history are again scarcely competent to explain the occurrence of long, orderly sequences of forms. The only effect of natural selection which is experimentally proven is its *conservative* effect in maintaining the species in its present equilibrium and at the maximum of its efficiency in the struggle for existence. That natural selection can produce a modificational effect is, like the inheritance of acquired characters, at present experimentally unproven.

A conspectus is given, showing roughly the relationships of the *Oenothera* species belonging to the group which contains the mutating forms.

In Section III. are summarized my studies on the present distribution of the mutating Oenotheras, and the history of their introduction from North America into European Botanic Gardens. They have now become naturalized in nearly all regions of the world. The early introductions into Europe can be identified in many cases by means of figures, descriptions, and specimens. Certain of these races appear to have resembled closely *O. Lamarckiana*, but no early record can be positively identified with this form to the exclusion of *O. grandiflora* or (in one case) *O. biennis*.

In Section IV. the mutation phenomena in *O. Lamarckiana* are considered in detail, the fact being emphasized and proven by illustrations that, although the ranges of variation of the various mutants frequently overlap in various characters, yet their modal conditions are different for each mutant, and the mutants are therefore clearly discontinuous in their origin from the parent form. When the mutants from *O. Lamarckiana* appear, their characters are fully developed in the first individual, and there is no evidence that subsequent selection from the offspring of a mutant has any effect in intensifying its characters.

Several of the mutant types, notably *O. gigas* and *O. nanella*, show a surprising range of variability, particularly in leaf-characters. The Oenotheras are also very sensitive to environmental changes, and the environment is a very important element in interpreting the wide range of fluctuation often observed in physiological

as well as structural characters. Particular races of *Oenothera* grown under different conditions of culture may be so unlike as scarcely to be recognizable, or indeed they may be wholly unrecognizable if the conditions of their cultivation are very diverse. These facts serve to emphasize the point of view that heredity and variation represent the two sides of a single process, namely the interaction of the organism with its environment in every stage of ontogeny.

Several races of *O. Lamarckiana* from various sources show constant differences from the form of DeVries's cultures, though some of them at least produce mutants analogous to those of DeVries. The differences between these *O. Lamarckiana* races are largely in the foliage, and they appear to be chiefly of a quantitative sort. The race of DeVries itself shows a considerable range of fluctuation, particularly in the crinkling of the leaves and the method of branching. *O. Lamarckiana* is thus a polymorphic species, containing several elementary species.

It is shown that in *O. Lamarckiana* and nearly all the mutants, three distinct leaf-types succeed each other in the ontogeny of the rosettes. This necessitates great care in comparing only corresponding stages of the various forms, a precaution which is especially urgent in comparing hybrids with their parent types. The mutant *O. gigas* usually does not show this succession of leaf-types, the young rosettes merely showing a succession of leaves of the same type but of increasing size. One race, however, received from the Botanic Garden at Palermo under the name *O. cognata*, whose adult rosette was identical with *O. gigas*, in my cultures of 1911 passed through stages apparently analogous to those of the other mutants.

One remarkable feature of the *Oenothera* mutants is the way in which the differing characters of leaf, stem, and flower remain together and refuse to be separated and redistributed by crossing as in Mendelian hybrids. The differences are not in single characters but affect every part of the plant, most of the former showing recognizable peculiarities from a very early stage right through their ontogeny. But many of the forms are more easily recognizable in certain stages than in others. Thus *O. brevistylis* shows marked peculiarities in the young seedlings, the mature rosettes are difficult to distinguish from *O. Lamarckiana*, but the adult plants are easily recognized by their bracts, sepals, and styles.

O. grandiflora, like the *O. Lamarckiana* forms, passes through several distinct stages in its rosette ontogeny, but under ordinary conditions of culture usually omits entirely the very characteristic adult stage of its rosette, and not infrequently the rosette stage is omitted altogether under the same conditions of culture in which it is produced in the *O. Lamarckiana* forms.

A large number of geographic races of *O. biennis* from North America have been grown. They differ chiefly in leaf-characters, but their behaviour in crossing is not yet known.

My cultures of *O. muricata* from many sources show that, especially in Canadian forms, a dimorphism exists which is comparable with the twin hybrids first observed by DeVries in crosses between *O. biennis* and *O. Lamarckiana*. These twin forms are respectively broad- and narrow-leaved, and they were observed in cultures from wild seeds collected in Nova Scotia, New Brunswick, and Manitoba. This indicates that the

explanation of the twin hybrids of DeVries is to be found in a fundamental alternative dimorphic condition present in many of the wild forms. It is further probable, as Honing thinks, that *O. Lamarckiana* and *O. rubrinervis* are twin types corresponding to the broad- and narrow-leaved forms.

Several years' cultures from a colony of Oenotheras naturalized on the coast of Lancashire near Birkenhead has shown that not only *O. Lamarckiana* and several of its mutants (as previously known), but also *O. grandiflora* and a host of other races previously unknown, occur in this locality. Many of the latter races have been isolated and several of them are found to breed true. Their bud characters are usually more or less intermediate between *O. Lamarckiana* and *O. grandiflora*, which indicates their hybrid origin. But they show the important fact that in *Oenothera*, hybrid races frequently form blends which breed true. Some of these races exhibit quite unexpected characters, and it remains to be determined whether a mutation factor in addition to hybridization is necessary to account for some of them—*i. e.*, whether, as in the case of *O. Lamarckiana* and its mutants, the characters of some of the races can not have originated merely through hybrid blending and splitting.

Numerous cultures of Oenotheras from Botanic Gardens, as well as data from other sources, have shown that the line of distinction between the large-flowered, long-styled and the small-flowered, short-styled forms is by no means so sharp as was formerly supposed. In certain large-flowered races which have undergone crossing the style may range from long to short in different flowers of the same plant. Wild species are also known having large flowers and short style, and others having small flowers with long style. There are in reality not merely two but a number of different lengths of style, ranging from long, as in *O. grandiflora* or *O. Lamarckiana*, to very short, as in *O. brevistylis*. And in each species or race there is usually a narrow range of fluctuation in length, which occasionally (apparently always in forms that have been crossed) becomes a remarkably wide range.

Oenothera hybrids show a variety of types of behaviour, depending upon the relationships of the forms concerned. Both blending and segregating types of inheritance occur, the former usually in interspecific crosses (though *O. gigas* shows this type of behaviour in some cases), and the latter usually in crosses between the mutants. Occasional mutants—e. g., *O. brevistylis* and *O. rubricalyx*—behave in typical Mendelian fashion. The twin hybrids, first described by DeVries and here illustrated for the first time, are produced when *O. biennis* and certain other species are pollinated by *O. Lamarckiana* or one of its derivatives. They are respectively broad- and narrow-leaved, and are called *laeta* and *velutina*. The *velutina* type crossed back with *Lamarckiana* gives *velutina*, *laeta*, and *Lamarckiana* in about the proportion 6 : 1 : 1. The twin types are, so far as known, intermediate between the parents in flower-characters, but divergent from either parent in leaf-characters. When self-pollinated they breed true, though it has been shown by DeVries that they produce two kinds of pollen-grains or egg-cells.

This type of inheritance, in which new, blended characters arise and breed true, occurs also in numerous interspecific and interracial crosses in *Oenothera*, and is probably of fundamental significance in connection with the origin of new races.

It is held that there is no fundamental distinction between mutations and fluctuations, except that one is inherited and the other is not—or, in other words, one is due to a germinal alteration, the other to a somatic variation.

VIII. Bibliography.

(This list includes only papers actually cited in the text.)

Andrews, F. M.—1910. Twin Hybrids (*laeta* and *velutina*) and their Anatomical Distinctions. Bot. Gazette, l. 193–201.

Artom, C.—1911. La sistematica del genere *Artemia* in relazione col numero dei cromosomi delle cellule sessuali e in relazione col numero e colla grandezza delle cellule somatiche. Biolog. Centralbl. xxxi. 104–108.

Bailey, Charles.—1907. De Lamarck's Evening Primrose (*Oenothera Lamarckiana*) on the sandhills of St. Anne's-on-Sea, North Lancashire. Address at Annual Meeting, Manchester Field-Club, pp. 28, pls. 6.

Bartlett, H. H.—1907. Some new Washington Plants. Bot. Gazette, xliv. 302–304.

—— 1911. Systematic Studies on *Oenothera*. I. *Oenothera Tracyi*, sp. nov. Rhodora, xiii. 209–211, pl. 93.

Bateson, W., E. R. Saunders, & R. C. Punnett.—1908. Experimental Studies in the Physiology of Heredity. Report IV. to the Evolution Committee of the Royal Society, pp. 40. London: Harrison & Sons.

Boulenger, G. A.—1907. On the Variations of the Evening Primrose (*Oenothera biennis*, Linn.). Journ. Botany, xlv. 353–363.

Boveri, Th.—1905. Zellenstudien: V. Ueber die Abhängigkeit der Kerngrösse und Zellenzahl der Seeigel-Larven von der Chromosomenzahl der Ausgangszellen. Jena: Gustav Fischer; pp. 80, pls. 2, text-figs. 7.

Davis, B. M.—1910. Notes on the Behaviour of certain Hybrids of *Oenothera* in the First Generation. Amer. Nat. xliv. 108–115.

—— 1911. Some Hybrids of *Oenothera biennis* and *O. grandiflora* that resemble *O. Lamarckiana*. Amer. Nat. xlv. 193–233.

DeVries, Hugo.—1901–3. Die Mutationstheorie. Leipzig. 2 Vols.

—— 1907. On Twin Hybrids. Bot. Gazette, xliv. 401–407.

—— 1908. Ueber die Zwillingsbastarde von *Oenothera nanella*. Ber. deut. Bot. Ges. xxvi. *a* 667–676.

—— 1909. Bastarde von *Oenothera gigas*. Ber. deut. Bot. Ges. *l. c.* pp. 754–762.

—— 1909. On Triple Hybrids. Bot. Gazette, xlvii. 1–8.

—— 1909. The Mutation Theory. Translated by Prof. J. B. Farmer and A. D. Darbishire. Chicago: Open Court Pub. Co.

—— 1911. Ueber doppeltreziproke Bastarde von *Oenothera biennis*, Linn., und *O. muricata*, Linn. Biolog. Centralbl. xxxi. 97–104.

Digby, L.—1912. The Cytology of *Primula kewensis* and of other related *Primula* Hybrids. Annals of Botany, xxvi. 357–388, pls. 41–44, figs. 2.

Gates, R. R.—1907. Pollen Development in Hybrids of *Oenothera lata* × *O. Lamarckiana*, and its relation to Mutation. Bot. Gazette, xliii. 81–115, pls. 2–4.

—— 1908. A Study of Reduction in *Oenothera rubrinervis*. Bot. Gazette, xlvi. 1–34, pls. 1–3.

—— 1909 *a*. The Behaviour of the Chromosomes in *Oenothera lata* × *O. gigas*. Bot. Gazette, xlviii. 179–199, pls. 12–14.

Gates, R. R.—1909 *b*. Apogamy in *Oenothera*. Science, n. s. xxx. 691–694.

—— 1909 *c*. An Analytical Key to some of the Segregates of *Oenothera*. 20th Rep. Missouri Botanical Garden, 123–137.

—— 1909 *d*. The Stature and Chromosomes of *Oenothera gigas*, DeVries. Arch. f. Zellforsch. iii. 525–552.

—— 1910 *a*. The Chromosomes of *Oenothera* Mutants and Hybrids. Reprint, Proc. 7th Internat. Zool. Congress, 1907, pp. 4.

—— 1910 *b*. The material basis of Mendelian Phenomena. Amer. Nat. xliv. 203–213.

—— 1910 *c*. Abnormalities in *Oenothera*. 21st Rep. Mo. Bot. Garden, xxi. 175–184, pls. 29–31.

—— 1911 *a*. Early Historico-botanical Records of the Oenotheras. Proc. Iowa Acad. Sci. 1910, 85–124, pls. 6.

—— 1911 *b*. Studies on the Variability and Heritability of Pigmentation in *Oenothera*. Zeitschr. f. ind. Abst- und Vererbungslehre, iv. 337–372, pl. 6.

—— 1911 *c*. Pollen Formation in *Oenothera gigas*. Annals of Botany, xxv. 909–940, pls. 67–70.

—— 1911 *d*. Mutation in *Oenothera*. Amer. Nat. xlv. 577–606.

—— 1912. An Onagraceous Stem without Internodes. New Phytol. xi. 50–53, pls. 2–3.

Gauchéry, P.—1899. Recherches sur le nanisme végétal. Ann. des Sci. nat., Bot. 8^{e} Série, ix. 61–156, pl. 4, figs. 32.

Geerts, J. M.—1909. Beiträge zur Kenntnis der Cytologie und der partiellen Sterilität von *Oenothera Lamarckiana*. Recueil des Travaux Bot. Néerlandais, v. 93–208, pls. 5–22.

—— 1911. Cytologische Untersuchungen einiger Bastarde von *Oenothera gigas*. Ber. deutsch. Bot. Ges. xxix. 160–166, pl. 8.

Giglio-Tos, Ermanno.—1908. L' eredita e le leggi razionali dell' ibridismo. Biologica, vol. ii. no. 10, pp. 1–36.

—— 1911. Les dernières expériences du Prof. DeVries et l'éclatante confirmation de mes lois rationelles de l'hybridisme. Biol. Centralbl. xxxi. 417–425.

Hill, A. W.—1912. The History of *Primula obconica*, Hance, under Cultivation, with some remarks on the History of *Primula sinensis*, Sab. Journ. of Genetics, ii. 1–20, pls. 1–2.

Honing, J. A.—1911. Die Doppelnatur der *Oenothera Lamarckiana*. Zeitschr. f. ind. Abst- und Vererbungslehre, iv. 227–278, figs. 10.

Jennings, H. S.—1911. Assortative Mating, Variability, and Inheritance of Size, in the Conjugation of *Paramecium*. Journ. Exp. Zoology, xi. 1–134.

Johannsen, W.—1909. Elemente der exakten Erblichkeitslehre. Jena: G. Fischer; pp. 517.

Leclerc du Sablon, Mathieu.—1910. Sur la théorie des mutations périodiques. Comptes Rendus, cli. 330–332.

Lutz, Anne M.—1909. Notes on the First Generation Hybrid of *Oenothera lata* ♀ × *O. gigas* ♂. Science, n. s. xxix. 263–267.

—— 1912. Triploid Mutants in *Oenothera*. Biol. Centralbl. xxxii. 385–435, figs. 7.

MacDougal, D. T.—1903. Mutations in Plants. Amer. Nat. xxxvii. 737–770, figs. 10.

MacDougal, Vail, Shull, & Small.—1905. Mutants and Hybrids of the Oenotheras. Carnegie Institution Pub. no. 24, pp. 57, pls. 22.

MacDougal, Vail & Shull.—1907. Mutations, Variations, and Relationships of the Oenotheras. Carnegie Institution Pub. no. 81, pp. 92, pls. 22, figs. 73.

Macoun, John.—1883. Catalogue of Canadian Plants. Montreal.

Marchal, Él. & Ém.—1909. Aposporie et sexualité chez les Mousses. II. Bull. de l'Acad. roy. de Belgique, 1909: 1249–1288.

—— 1911. Aposporie et sexualité chez les Mousses. III. Bull. de l'Acad. roy. de Belgique, 1911: 750–778, pl. 1.

Nelson, Aven.—1911. Contributions from the Rocky Mountain Herbarium. IX. New Plants from Idaho. Bot. Gazette, lii. 261–274.

Nilsson, N. Heribert-.—1909. *Oenothera gigas*, framgången som mutation i Sverige. Bot. Notiser, 1909, 97–99.

—— 1912. Die Variabilität der *Oenothera Lamarckiana* und das Problem der Mutation. Zeitschr. f. Abst- und Vererbungslehre, 8 : 89–231, pls. 3–5, figs. 36.

Saunders, Edith R.—1910. Studies in the Inheritance of Doubleness in Flowers. I. *Petunia*. Journ. of Genetics, i. 57–69, figs. 5.

Schouten, A. R.—1908. Mutabiliteit en Variabiliteit. Dissertation : Groningen ; pp. 196.

Stomps, Theo. J.—1912. Die Entstehung von *Oenothera gigas*, DeVries. Ber. deutsch. Bot. Ges. xxx. 406–416.

Strasburger, E.—1910. Chromosomenzahl. Flora, c. 398–446, pl. 6.

Tischler, G.—1908. Zellstudien an sterilen Bastardpflanzen. Arch. f. Zellforsch. i. 33–151.

—— 1910. Untersuchungen über die Entwicklung des Bananen-Pollens. I. Arch. f. Zellforsch. v. 622–670, pls. 30–31, figs. 4.

Vail, Anna M.—1905. *Onagra grandiflora* (Ait.), a Species to be included in the North American Flora. Torreya, v. 9–10.

Zeijlstra, H. H. Fzn.—1911. *Oenothera nanella*, DeVries, eine krankhafte Pflanzenart. Biol. Centralbl. xxxi. 129–138, figs. 5.

—— 1911. On the Cause of Dimorphism in *Oenothera nanella*. Kon. Akad. Wetens. Amsterdam, 1911 : 680–685, figs. 3.

IX. EXPLANATION OF THE PLATES.

The figures representing whole mature plants, or shoots in flower or fruit, were reproduced without reduction from the size of the original photographs. All others were reduced one-third. The buds were all originally photographed natural size, and are therefore reduced to two-thirds natural size in reproduction.

Plate 1.

Fig. 1. *O. Lamarckiana*, young seedlings.

2, 3. *O. Lamarckiana*, young rosettes.

4. *O. Lamarckiana*, older rosette, showing three leaf-types (see text).

5. *O. Lamarckiana*, mature rosette.

6. *O. Lamarckiana*, selected leaves from mature rosettes, showing range of fluctuation.

7. *O. Lamarckiana*, adult plant. An extreme variant having very much crinkled leaves.

8. The same, another individual. Terminal shoot in bloom, upper stem-leaves practically without crinkles.

9. Young seedlings of another race of *O. Lamarckiana* found in St. Louis, Mo.

10. Mature rosette of St. Louis race of *O. Lamarckiana*. *Cf.* figs. 4 and 5 showing the *O. Lamarckiana* of H. DeVries.

11. Adult plant of same race as last. *Cf.* figs. 7 and 8.

12. A rosette from a culture of "*O. Lamarckiana* var. *cruciata*," from the Bremen Botanic Garden. The mesophyll of the leaf develops on only one side of the midrib, the other half curving around to form a sickle-shaped blade.

13, 14. Developing rosettes of *O. laevifolia*. The figures represent the *same plant* taken at an interval of 8 days, to show how new leaves appear. They show the three types of rosette-leaf described in text.

Plate 2.

Fig. 14. See last Plate, No. 13.

15. *O. laevifolia*, young seedlings. *Cf.* figs. 1, 21, 25, 83.

16–17. Rosettes of *O. laevifolia*. The latter is typical, while the former is much crinkled and scarcely distinguishable from *O. Lamarckiana* in a photograph. *Cf.* figs. 4 and 5. Fig. 16 also shows the three ontogenetic leaf-types.

18. *O. laevifolia*, selected leaves from mature rosettes, showing range of variation in leaf-width and crinkling. *Cf.* figs. 6, 23, and 33.

19. Typical flowering-shoot of *O. laevifolia*. Leaves narrower, smoother, and more furrow-shaped than *O. Lamarckiana*. *Cf.* figs. 7 and 8.

20. *O. laevifolia*, shoot in fruit. *Cf.* figs. 31, 52, 77, and 80.

21. *O. brevistylis*, young seedling. *Cf.* fig. 15, *O. laevifolia*, same age; also figs. 1 and 25.

22. Mature rosette, *O. brevistylis*. Each such rosette contains some leaves with broad, rounded tips. *Cf.* fig. 5 (*O. Lamarckiana*).

23. Selected leaves from mature *O. brevistylis* rosettes, showing range of variation. *Cf.* fig. 6 (*O. Lamarckiana*) and fig. 18 (*O. laevifolia*).

24. Buds of *O. brevistylis*, two-thirds natural size, sepal tips very short.

25–26. *O. rubricalyx*.

25. Young seedlings. *Cf.* fig. 1 (*O. Lamarckiana*).

26. Typical rosette of *O. rubricalyx*. *Cf.* fig. 4.

27. *O. rubrinervis* rosette, leaf-tips broader than typical.

Plate 3.

Fig. 28. "Lateral rosette" from a plant of *O. rubrinervis* whose stem was bent horizontally and afterwards developed a number of rosettes in place of lateral branches.

29. Flowering shoot of *O. rubrinervis*, from *O. rubrinervis* × *O. Lamarckiana*.

30. *O. rubricalyx*, adult plant, grown in heavy clay soil and devoid of lateral branches.

31. Fruiting shoot of same, showing capsules and bracts.

32. *O. gigas*, typical young rosette, showing nearly orbicular thick leaf-blades.

33. *O. gigas*, leaves from mature rosettes, showing range of variation in a culture grown in 1909.

34. Rosette of *O. gigas*, broad-leaved type.

35. Rosette of *O. gigas*, an extreme variant with very narrow, almost linear leaves.

36–37. *O. gigas*, narrow-leaved rosettes.

38. *O. gigas*, buds, two-thirds natural size, much larger than those of other mutants. *Cf.* figs. 24, 41, 43, 49, and 53.

39. *O. gigas nanella*, a dwarf form of *O. gigas*.

40. *O. cognata*, Palermo Botanic Garden. Earlier rosette-leaves with long petioles, later ones identical with *O. gigas*. An independent mutation.

41. *O. nanella*, buds, two-thirds natural size, with bract attached to one.

42. *O. lata*, typical rosette from the race of DeVries.

43. Buds, two-thirds natural size.

Buds 1–3 (on the left), *O. lata* of DeVries, which produces almost no good pollen.

Buds 4–7 (on the right), from a race of *O. lata* or *O. semilata* from Lancashire, producing pollen. The sterility of the pollen is accompanied by crumpling of the petals and consequent distortion of the buds.

Plate 4.

Fig. 44. Rosette of *O. semilata* or *O. lata* from Lancashire.

45. Lancashire Oenotheras, a race of *O. grandiflora* from Lancashire. Rosette in tropical hothouse, age 4 months.

46. Same as last, 6 weeks later. A new type of rosette-leaf has appeared, which is characteristic of *O. grandiflora,* but is usually omitted altogether in ordinary cultures of this species.

47. *O. grandiflora* race from Lancashire. Mature rosette in hothouse, age 9 months. *Cf.* fig. 46.

48. Adult plant of *O. grandiflora* from Alabama, under ordinary conditions of culture at Mo. Bot. Garden. It produces no rosette but branches freely, giving the plant a shrubby appearance.

49. Buds, two-thirds natural size, from a Lancashire race of *O. grandiflora.* They are smooth and free from hairs, rounded, with thin papery sepals. *Cf.* fig. 24.

50. Rosette of a race of *O. biennis* from New York State; photographed from a culture at Woods Hole, Mass. This pure race was used in my hybrids with *O. Lamarckiana* and other forms.

51. Flowering shoot of the same.

52. Shoot of the same in fruit, showing capsules and bracts.

53. Buds of the same, two-thirds natural size, showing diminution in size of bracts.

54. Broad-leaved rosette of *O. muricata* from Nova Scotia.

55. Narrow-leaved rosette of *O. muricata* from Winnipeg, Manitoba. Both these races occur together with identical characters in both these localities. See text, p. 40.

56. Flowering stage of broad-leaved type of *O. muricata* from Winnipeg. It will be seen that the rosette is identical with fig. 54, but reduced in size in reproduction.

Plate 5.

Fig. 57. Very young rosette of *O. ammophila,* which, in this stage at least, is identical with certain narrow-leaved races of *O. muricata,* such as represented in the next figure.

58. Rosette of a uniform race of *O. muricata* from Seal Harbour, Maine.

59. Lancashire Oenotheras. Rosette No. 5 from culture in tropical hothouse; between *O. lata* and *O. semilata,* age 9 months. This plant was fertile. See text.

60. Lancashire Oenotheras, No. 8. Rosette in tropical hothouse, age $9\frac{1}{2}$ months.

61. Same culture as last, No. 18, age 4 months.

62. Same culture as last, No. 22, age 5 months, a dwarf rosette with characteristic type of leaf.

63. Lancashire Oenotheras, No. 23. Rosette in tropical hothouse, age 4 months. *Cf.* fig. 45, from which it differs in having longer petioles and narrower blades.

64. Lancashire Oenotheras, No. 25. Rosette in tropical hothouse, age $9\frac{1}{2}$ months. This has since given rise to a characteristic race. (*Cf.* Gates, 1911 *b*, p. 350.)

65. Same culture as last, No. 33, age $9\frac{1}{2}$ months.

66. Type 2 in F_1 from No. 5 of Lancashire Oenotheras. The rosette closely resembles DeVries's *O. elliptica.* See p. 45.

67. Type 4 in F_1 from No. 5 of Lancashire Oenotheras. Adult plant, showing small flowers with short style. See p. 45.

68. A pan of seedlings showing the F_1 from *O. lata* × *O. nanella.* The forms represented are *O. Lamarckiana, O. rubrinervis, O. nanella,* and an aberrant (colourless) type. See text, p. 50.

69. Rosette of *O. biennis* × *O. Lamarckiana,* F_1, broad-leaved or *laeta* form.

70. Rosette of *O. biennis* × *O. Lamarckiana,* F_1, narrow-leaved or *velutina* form.

Plate 6.

Fig. 71. Rosette of *O. biennis* × *O. laevifolia*, F_1, broad-leaved type. *Cf.* fig. 69.
72. Rosette of *O. biennis* × *O. laevifolia*, F_1, narrow-leaved type. *Cf.* fig. 70.
73. Intermediate type from *O. biennis* × *O. laevifolia*, F_1, another cross.
74. Flowering shoot of *O. biennis* × *O. Lamarckiana*, F_1, *velutina* type.
75. Flowering shoot of *O. biennis* × *O. Lamarckiana*, F_1, *laeta* type.
76. Buds, two-thirds natural size, from *O. biennis* × *O. Lamarckiana*, F_1 (*velutina*). *Cf.* bracts and buds with fig. 53 (*O. biennis*). The buds are larger and more hairy, the bracts more nearly entire.
77. Shoot showing flowers, capsules, and bracts from *O. biennis* × *O. laevifolia*.
78. Rosette of *O. Lamarckiana* × *O. biennis*, F_1, broad-leaved type. *Cf.* fig. 69.
79. Rosette of *O. nanella* × *O. biennis*, F_2.
80. *O. Lamarckiana* × *O. biennis*, shoot in fruit showing capsules and bracts. *Cf.* figs. 77 and 31.
81. Pan of seedlings of *O. biennis* × *O. nanella*, F_1. *Cf.* figs. 82 and 83, same age.
82. Pan of seedlings of *O. nanella* × *O. biennis*, F_1.
83. *O. nanella*, pan of young seedlings. *Cf.* figs. 81 and 82, same age.

Note *added January 2nd*, 1913.

The recent important paper of N. Heribert-Nilsson (1912) has shown that in an independent race of *O. Lamarckiana* obtained from a garden in Southern Sweden, which differs in some respects from the race of DeVries, mutations are produced which are parallel to, though differing from, the DeVriesian mutants. Thus it is further shown that *O. Lamarckiana*, like ordinary wild species, contains various elementary species, and new difficulties arise before those (*e. g.*, B. M. Davis) who would derive all the races of *O. Lamarckiana* from a single (hypothetical) source.

Nilsson also expresses the view, with which I am in agreement, that from an evolutionary standpoint it is immaterial just what forms may have taken part in the complex ancestry of *O. Lamarckiana*.

The valuable data of Nilsson's paper, and particularly his description of the behaviour of a new giant type, are of great interest. His explanation of the mutation phenomena without regard to the cytological facts has, however, led him into theoretical errors which might otherwise have been avoided, but these in no way detract from the usefulness of the mass of breeding data contributed. I shall refer in greater detail to these giant forms in a paper now in the press in the 'Biologisches Centralblatt.'

R. R. G.

1

2

3

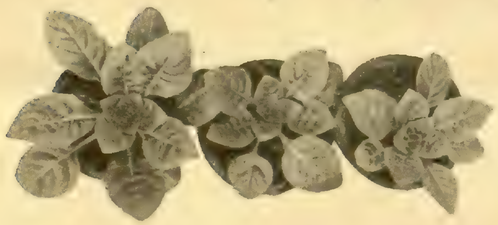
4

5

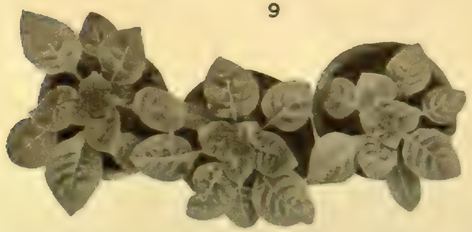
6

7

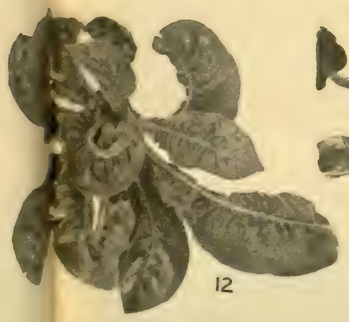
8



9



11



12

10

13

R. R. Gates, phot.

MUTANTS OF OENOTHERA.

Grout, sc. et imp.

14

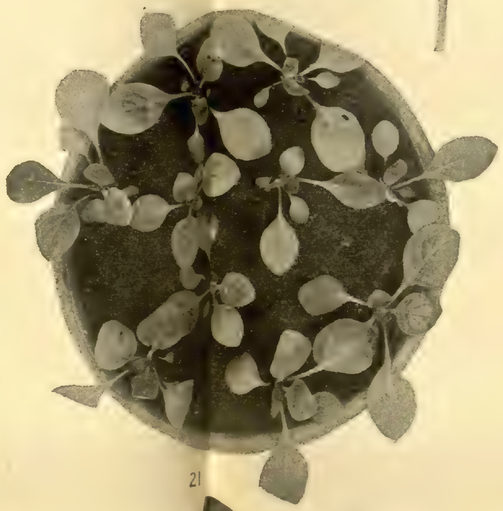
17

18

23

15

19



21

24

25

16

22

26

27

R. R. Gates, phot.

MUTANTS OF OENOTHERA.

Grout, sc. et imp.

28

32

33

36

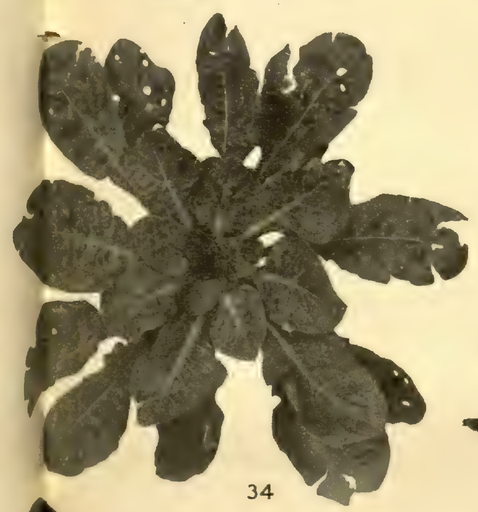
37

29

30

38

31



34

35

42

39

40

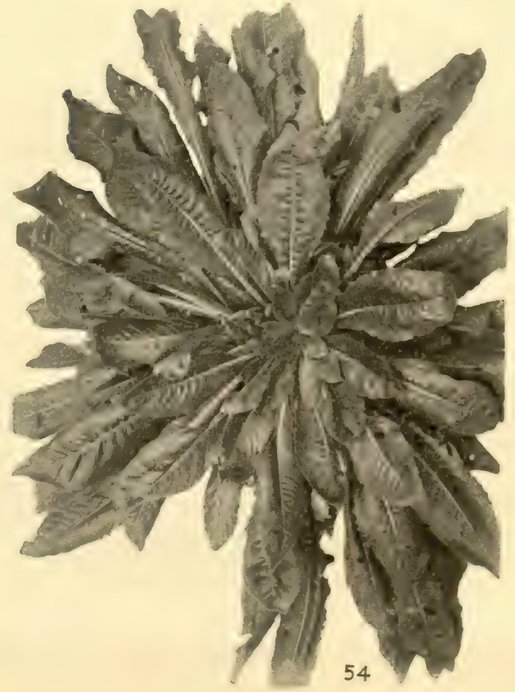
41 43

44

45

50

53



54

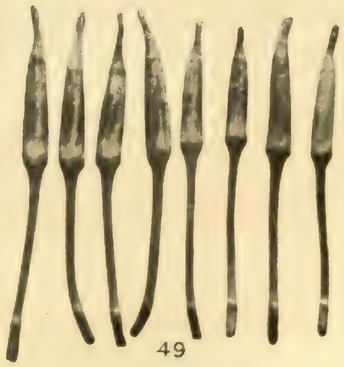
46

48

52

51

56



49

55

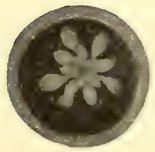
47

R. R. Gates, phot

MUTANTS OF OENOTHERA.

Groat, sc. et imp

58



57

60

62

64

59

61

63

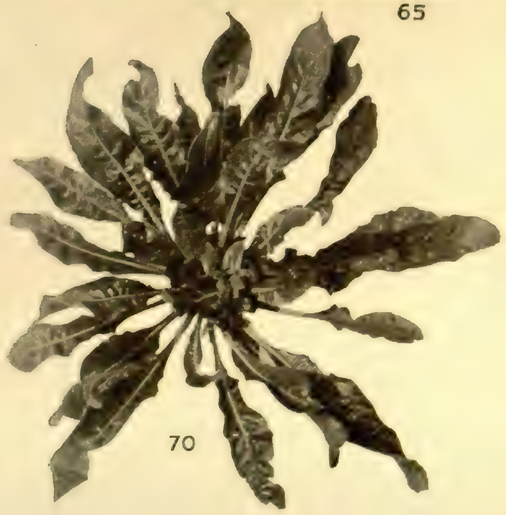
65

67

66

68

69



70

R. R. Gates, phot.

MUTANTS OF OENOTHERA.

Grout, sc. et imp

74

71

73

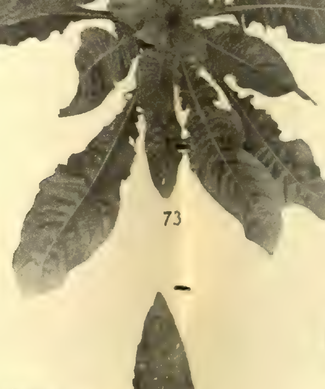
79

75

72

76

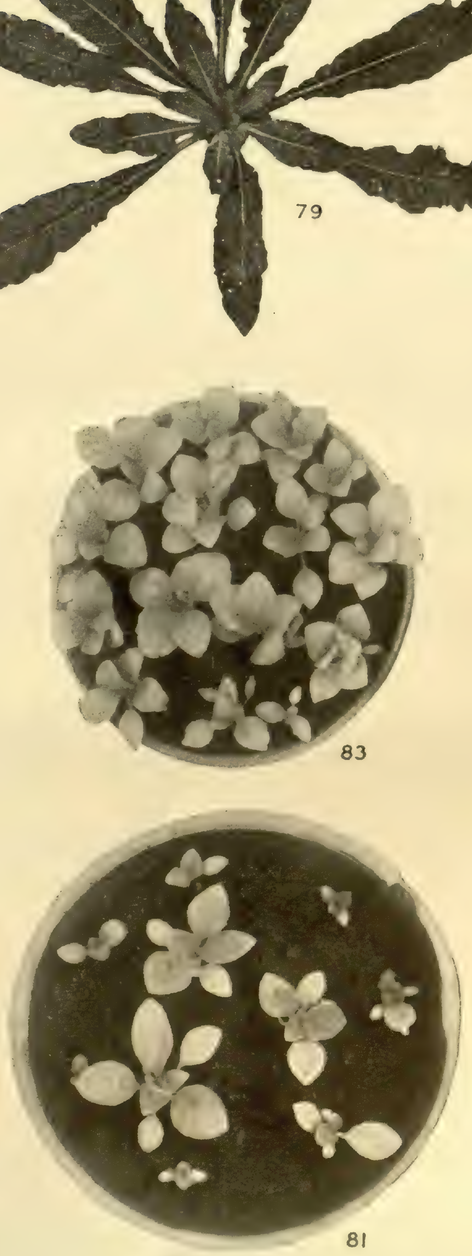
78



82

77

83



81

80

R. R. Gates, phot.

MUTANTS OF OENOTHERA.

Grout, sc. et imp.

LINNEAN SOCIETY OF LONDON.

MEMORANDA CONCERNING TRANSACTIONS.

The First Series of the Transactions, containing both Botanical and Zoological contributions, has been completed in 30 Vols., and a few entire sets are still for sale. Only certain single volumes, or parts to complete sets, may be obtained at the original prices. The price of the Index to Vols. 1–25 is 8*s.* to the public, and 6*s.* to Fellows; to **Vols. 26–30, 4*s.* to the public, and 3*s.* to Fellows.**

The Second Series of the Transactions is divided into Zoological and Botanical sections. The prices of the Botanical parts of these which have been published are as under-mentioned. (For the Zoological parts see Zoological wrapper.)

Second Series.—Botany.

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
I.	Parts I.–IX. (complete).						
	1875–80.	8	1	0	6	1	6
II.	Parts I.–XVI. (complete).						
	1881–88.	6	16	10	5	2	9
III.	Part I. 1888.	3	12	0	2	14	0
	Part II. 1891.	0	5	0	0	3	9
	Part III. 1891.	0	7	0	0	5	0
	Part IV. 1891.	0	6	0	0	4	6
	Part V. 1891.	0	6	0	0	4	6
	Part VI. 1891.	0	3	6	0	2	8
	Part VII. 1892.	0	6	0	0	4	6
	Part VIII. 1893.	0	6	0	0	4	6
	Part IX. 1893	1	8	0	1	1	0
	Part X. 1894.	0	10	0	0	7	6
	Part XI. 1894.	0	3	4	0	2	6
IV.	Part I. 1894.	1	0	0	0	15	0
	Part II. 1894.	2	0	0	1	10	0
	Part III. 1895.	2	10	0	1	17	0
	Part IV. 1895.	0	3	4	0	2	6
V.	Part I. 1895.	0	9	0	0	6	9
	Part II. 1895.	0	12	0	0	9	0
	Part III. 1896.	0	6	0	0	4	6
	Part IV. 1896.	1	0	0	0	15	0
	Part V. 1896.	0	14	0	0	10	6
	Part VI. 1896.	0	4	0	0	3	0
	Part VII. 1897.	0	4	0	0	3	0
	Part VIII. 1897.	0	6	0	0	4	6
	Part IX. 1899.	0	12	0	0	9	0
	Part X. 1899.	0	6	0	0	4	6
	Part XI. 1899.	0	7	0	0	5	0
	Part XII. 1899.	0	12	0	0	9	0
	Part XIII. 1900.	0	1	6	0	1	2
	Part XIV. 1900.	0	3	0	0	2	3
	Part XV. 1901.	0	6	0	0	4	6

Second Series.—Botany (*continued*).

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
VI.	Part I. 1901.	1	10	0	1	2	6
	Part II. 1901.	0	6	0	0	4	6
	Part III. 1902.	0	18	0	0	13	6
	Part IV. 1903.	0	8	0	0	6	0
	Part V. 1903.	0	8	0	0	6	0
	Part VI. 1903.	0	12	0	0	9	0
	Part VII. 1904.	0	12	0	0	9	0
	Part VIII. 1904.	0	12	0	0	9	0
	Part IX. 1904.	0	7	0	0	5	3
	Part X. 1904.	0	14	0	0	10	6
	Part XI. 1905.	0	4	0	0	3	0
VII.	Part I. 1904.	0	5	0	0	3	9
	Part II. 1905.	0	6	0	0	4	6
	Part III. 1906.	0	3	0	0	2	3
	Part IV. 1906.	0	7	0	0	5	3
	Part V. 1907.	0	10	0	0	7	6
	Part VI. 1907.	0	4	0	0	3	0
	Part VII. 1907.	0	6	0	0	4	6
	Part VIII. 1908.	0	5	0	0	3	9
	Part IX. 1908.	0	2	6	0	2	0
	Part X. 1908.	0	7	0	0	5	3
	Part XI. 1909.	0	4	0	0	3	0
	Part XII. 1909.	0	12	0	0	9	0
	Part XIII. 1909.	0	5	0	0	3	9
	Part XIV. 1909.	0	6	0	0	4	6
	Part XV. 1910.	0	6	0	0	4	6
	Part XVI. 1912.	0	3	0	0	2	3
	Part XVII. 1912.	0	8	0	0	6	0
	Part XVIII. 1912.	0	5	0	0	3	9
	Part XIX. 1912.	0	3	0	0	2	3
	Part XX. Index. (In the Press.)						
VIII.	Part I. 1913.	1	0	0	0	15	0

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

---

1. ON SOME INDIAN JURASSIC GYMNOSPERMS,

AND

2. RHEXOXYLON AFRICANUM, A NEW MEDULLOSEAN STEM.

BY

NELLIE BANCROFT, B.Sc. (Lond.), F.L.S.,
1851 RESEARCH SCHOLAR, NEWNHAM COLLEGE, CAMBRIDGE.

LONDON:

PRINTED FOR THE LINNEAN SOCIETY

BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON-HOUSE, PICCADILLY, W.,

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

May 1913.

II. *On some Indian Jurassic Gymnosperms.*

By Nellie Bancroft, *B.Sc.(Lond.), F.L.S.*, 1851 *Research Scholar, Newnham College, Cambridge.*

(Plates 7–9.)

Read 21st November, 1912.

I. Introduction.

The fossil plants under consideration are contained in four siliceous blocks sent by Mr. Hayden, Director of the Geological Survey of India, at the request of Professor Seward *. The strata from which the blocks were obtained belong to the Rajmahal Series, a division of the Upper Gondwana Group, and are probably of approximately the same age as the Lower Jurassic (Liassic) rocks of Europe (4, 18, 15). The Rajmahal Series of strata is best developed in Bengal, north of Calcutta, and takes its name from the Rajmahal Hills, where it was first recognised. It also occurs in the Southern Godavri district and in the south and south-west of Madras. The fossil plants now to be described came from the Rajmahal Hills, the exact locality being Amrapara, on the Bansloi River, Puchwara Pass. The geology of the district has been described by Oldham and Morris (19); more fully, with an accompanying map, by Ball (1); by Medlicott and Blanford (15); and by R. D. Oldham (18).

The blocks (referred to in the sequel as I., II., III., IV.) are closely packed with cycadean fronds; they contain also cycadean stem-fragments, a fructification, a probable fructification-axis, and numerous coniferous branches. Similar Jurassic plants have been figured and described by Messrs. Oldham and Morris and by Dr. Feistmantel in the Memoirs of the Geological Survey of India. Indeed, several of the outstanding features of the four blocks have been already noted by these writers.

Oldham and Morris (19) figure the frond on the under surface of block I. (*cf.* their pl. 21. fig. 3 with Pl. 9. fig. 3 *a*); also the stem-structures on blocks I. and II. (*cf.* their pl. 34. figs. 2 & 3 with Pl. 9. figs. 4 & 1). The impression on block IV. (Pl. 7. fig. 1) is similar to that shown by Oldham and Morris, pl. 34. fig. 1. Feistmantel (7, p. 78) describes the block II. stem, noting the similarity to Carruthers's figures of *Bucklandia Milleriana* and some species of *Yatesia*, which show alternating zones of large and small leaf-scars. He cannot decide, however, whether this character is accidental or constant in the Rajmahal stems, which, he points out, have generally only the larger scars and are somewhat like those drawn by Williamson (40, pl. 53. fig. 5). The same author (6, Taf. 3, fig. 1 *a* & *b*) gives figures of the stem and fructification contained in block II. (Pl. 9. fig. 1; Pl. 7. fig. 2). He refers the stem to *Williamsonia*, and considers the

* [I take this opportunity of thanking my friend Mr. Hayden for his ready response to my request for permission to borrow the specimens, and to have sections cut from the blocks.—A. C. Seward.]

fructification to be probably that of *W. gigas*, on account of the large number of bracts which surround it.

Professor Seward (27, pp. 193, 194; text-fig. 30) describes a British Museum specimen of an Indian cycadean stem from the Upper Gondwana Series. This agrees very closely with the stem-fragment in block I. (Pl. 9. fig. 4), both externally and in anatomical structure (*cf.* 27, text-fig. 30 B and Pl. 8. figs. 9 & 10). The fronds of *Ptilophyllum cutchense* (27, p. 195; text-fig. 32) in connection with this stem are identical with many of those in the Amrapara blocks (*cf.* Pl. 9. fig. 3).

II. Methods of Examination of the Blocks.

The blocks consist of a very hard and compact porcellanous substance, the result of the metamorphism by igneous rocks, of very fine close shales (19, p. 4). Tests with acid showed that this "porcellanite" is very largely, if not entirely, composed of silica, for it dissolved readily in dilute hydrofluoric acid, while dilute hydrochloric acid failed to reveal any trace of limy substance.

The very complete silicification of the plant-remains enclosed in the blocks renders them unsuitable for satisfactory microscopic examination in thin sections, these being extremely transparent. Various attempts were made to overcome this difficulty, such as staining the sections with fuchsin; the use of coloured screens in the condenser of the microscope; examination by polarised light and by dark ground illumination; and the examination of sections cleared of Canada balsam, and mounted in media of different refraction, *e.g.*, cedar-wood oil and water.

None of these methods were, however, wholly satisfactory, the transparent and homogeneous nature of the material rendering impossible, in most sections, an investigation of the finer anatomical details. In some cases, smooth cut surfaces were etched with dilute hydrofluoric acid in the hope that this would reveal differences in the degree of silicification, and thus facilitate examination by reflected light. This method also was unsuccessful, for silicification and a certain amount of metamorphism due to contact with igneous material have evidently obliterated much of the structure, and hence little differentiation was apparent on the etched surfaces.

Finally, surfaces from which sections had been cut were treated with immersion oil without previous etching. Such surfaces, examined by reflected light and considered in conjunction with their corresponding sections, provided the means by which all the evidence with regard to anatomical structure was obtained.

Professor Nathorst's collodion-film method (17) was used to elucidate the surface-features of some of the leaves present in the blocks. It was determined that the cells above the course of the vascular bundles are elongated and that those between are shorter and more isodiametric (Pl. 7. fig. 10). No certain evidence with regard to form and distribution of stomata can be obtained from a surface-film of this kind, especially if the stomata are at all sunk. In this case it is possible that some apparent cell-groups represent stomata-openings surrounded by epidermal cells (Pl. 7. fig. 11; *cf.* stoma-opening of *Macrozamia corallipes*, fig. 12).

III. Descriptions of the Specimens.

A. Coniferous Remains.

Brachyphyllum, Brongn.

Brachyphyllum mamillare, Brongn.

All the blocks contain fragmentary remains of foliage-shoots. The leaves of these shoots are small and fleshy, triangular in shape, with a median dorsal keel, crowded, and more or less spirally arranged; in some cases a small dot-like protuberance may be seen towards the apex of the leaf (Pl. 7. fig. 6). The name *Brachyphyllum mamillare*, Brongn. (2, p. 109), has been applied by various writers to coniferous remains of this type, *Thuites expansus*, Phill. (20; see also 13), and *Echinostrobus expansus*, Feistm. (6), being apparently synonymous (see Seward, 27, pp. 297 and 298 for further references). As Seward (30, p. 148) remarks, it is not always easy to decide whether coniferous twigs of the above type should be referred to *Brachyphyllum* or *Thuites*, and though a distinction has been made between the genera, in that *Brachyphyllum* should have spiral phyllotaxy and *Thuites* whorled, this seems to be a variable character, at least in *Thuites*, a departure from the whorled arrangement being frequently noted (30, p. 140). The generic name *Sphenolepidium* has also been applied to coniferous twigs similar in habit to the Indian specimens, though possessing, perhaps, less markedly adpressed leaves. Oldham and Morris have referred similar examples from Amrapara to *Arthrotaxites indicus* (19, pl. 32. fig. 8).

In the present case, however, the generic name *Brachyphyllum* has been adopted, as it does not infer, like *Thuites* or *Arthrotaxites*, any relationships with recent genera. Seward (23, p. 214) points out that the genus "has been compared with several recent genera; but we cannot regard *Brachyphyllum*, with its numerous species from various geological horizons, as more than a purely provisional genus, the actual botanical nature of which is very uncertain, probably more than one family of Coniferæ being represented by the forms referred to under this name."

Further, on account of their similarity to *B. mamillare*, these Indian forms may be referred to that species, which also is regarded as provisional.

With regard to systematic position, the similarity of habit of *Brachyphyllum* to that of certain Cupressineæ has suggested comparison with that group, while Hollick and Jeffrey (11) have definitely referred *B. macrocarpum*, Newberry, to the Araucarineæ on anatomical grounds, making Brachyphylloideæ a sub-tribe of the wider group (11, p. 75). They do not, however, suggest that all the species of *Brachyphyllum* should be included under that head (p. 34). For the present, however, the Indian coniferous remains referred to *Brachyphyllum mamillare* may be considered as of doubtful affinity, too little being known of their anatomical structure and organs of fructification to render more definite classification advisable.

It may be noted that sections and cut surfaces of the blocks show transverse and

longitudinal sections of the leafy twigs (Pl. 7. figs. 3*f* & 7). No structure can be definitely determined, though the impression is given of leaves surrounding a central stem, the leaf-sections having a vascular bundle, a fair amount of palisade mesophyll, and a definite epidermis. In general outline and arrangement of parts there is agreement with sections of the leafy twigs of some recent Cupressineæ, but this, of course, is to be expected from the form of the twigs.

Coniferous Wood.

In blocks II. and III. there are several examples of coniferous wood (Pl. 8. fig. 17 *b*), which in section shows, more or less indefinitely, narrow medullary rays and bordered pits, such as Hollick and Jeffrey figure for *Brachyoxylon notabile* (*cf.* 11, p. 56, pl. 13. fig. 3, with Pl. 7. fig. 8). No examples of flattened or alternating pits were seen. There is the possibility that the wood originally belonged to the same plant as the leafy twigs, though there is no evidence of this beyond the association of the plant-remains in the blocks. The wood is fragmentary and too ill-preserved to allow of reference to any genus or species.

Coniferocaulon, Fliche.

Coniferocaulon sp.

Block III. shows a portion of a large stem, 14 cms. long by 10 cms. wide (Pl. 9. fig. 2). The stem has externally the appearance of a *Zamia* without leaf-bases, *e. g.*, *Z. Skinneri* or *Z. Loddegesii* (Seward, 24, pl. 14, figs. 1 & 2). The surface is irregularly grooved in a transverse direction, with occasional elliptical protuberances. No leaf-scars can be distinguished. The interior of the stem is occupied by a much-shattered woody cylinder. What appears to be the reverse of the external layers of this stem is represented on the surface of the block (Pl. 7. fig. 19).

Seward refers to a Lower Greensand type showing external characters somewhat similar to those of the Indian stem, as *Benstedtia* (24), substituting this name as not implying any particular affinity, for the more definite name *Dracæna Benstedtii* given by König, following Mackie's suggestion that the stem was very like that of a *Dracæna* (14). Fliche (10) figures a stem-fragment from the Lower Cretaceous of Saint-Dizier, similar externally to the stem described above. He notices the resemblance, in the external features at least, to the Araucarias of the Colymbæa section, and definitely refers the stem to the Araucarian Coniferæ (p. 7), naming it *Coniferocaulon colymbeæforme.*

A similar stem is recorded from the Uitenhage Series of South Africa (Upper Jurassic or Wealden Age). It is compared with Fliche's stem, but the name *Benstedtia* is adopted as the more non-committal term (29, p. 34; pl. v. fig. 2; text-fig. 5). In his description of the Jurassic Flora of Sutherland, however, Seward (31, p. 690, pl. ix. fig. 41) refers a stem showing externally irregular transverse wrinklings to *Coniferocaulon*, on account of the narrowness of the pith, a character which suggests coniferous affinities rather than cycadean. In a footnote he mentions that Dr. Stopes, in the course of her examination of the British Museum Benstedtias, has found traces of xylem elements with pits of

coniferous type. Dr. Stopes herself (32) in a recent paper concludes that the so-called Benstedtias are merely the decayed remains of gymnospermous types of higher coniferous affinities, and includes them under the name *Coniferocaulon Benstedtii*. Still more recently Knowlton (12) proposes to substitute the name *Benstedtia Benstedti* for these types, since, according to him, the rules of nomenclature will not permit Dr. Stopes's combination of generic and specific terms. Dr. Stopes has replied to this criticism (33) by pointing out that the types variously referred to *Benstedtia* and *Coniferocaulon* do not constitute a genus at all, as they are merely fragments referable to coniferous stems, and that her use of the term *Coniferocaulon Benstedtii* is merely for the sake of convenience and historic interest.

In the present case, on account of external similarity to these plant-fragments, the block III. "stem" is provisionally referred to the Coniferæ under the designation *Coniferocaulon* sp., that genus being used in Dr. Stopes's sense of the term (32, p. 59) as a convenient and non-committal means of referring to fragments of stems of higher coniferous affinities.

B. Cycadean Remains.

i. *Fronds.*

Ptilophyllum, Morris.

Ptilophyllum cutchense, Feistm.
Ptilophyllum acutifolium (Oldh. & Morris).

Block I. (Pl. 9. fig. 3 *a*) shows the remains of a pinnate frond; the pinnæ appear as *impressions* on either side of the rachis, upon which their scars of attachment are to be seen (Pl. 8. fig. 1; *cf.* 19, pl. 21. fig. 5 *a*). This impression was about 9 cms. long before the block was cut and represented probably almost the whole length of the original frond, since the pinnæ decrease in size towards either end of the fragment (4, p. 13). This frond is figured by Oldham and Morris (19, pl. 21. fig. 3) as *Ptilophyllum cutchense* (see Feistmantel, 4, p. 13, and 5, pp. 42 & 43, for synonyms). Other examples are distinctly referable to *Ptilophyllum*, but differ somewhat from the typical *P. cutchense*. Feistmantel (4 and 5) unites these varieties as the "Group of *Ptilophyllum cutchense*," characterized by short oblique pinnæ, a little curved, and obtusely acuminate, slightly auriculate at the base, imbricate or contiguous, subalternately and obliquely inserted on the rachis. At *b* on the photograph (Pl. 9. fig. 3) is the impression of a frond-apex, while *d* is apparently the true upper surface of a frond (Pl. 9. fig. 3; Pl. 8. fig. 2). The apex of a frond is also shown on Pl. 8. fig. 3.

The frond *c* seems to be of a different type, and agrees with Feistmantel's diagnosis of *Ptilophyllum acutifolium*, Morris (4, p. 11), being distinguished from *P. cutchense*, Morris, by its longer, narrower pinnæ forming a larger frond. The pinnæ are more acuminate and curved than in the allied species, and are clearly subauriculate at the upper basal angle, and decurrent at the lower (Pl. 8. fig. 5; *cf.* 4, Taf. 1 and Taf. 2. figs. 1–4).

There are several examples of this type in block I., it being, according to Feistmantel (5, p. 45), of frequent occurrence in the Rajmahal Hills.

The venation of the *Ptilophyllum* pinnæ is of an ordinary cycadean type, there being no midrib (Pl. 8. fig. 4 *a*). The nerves are parallel and apparently end blindly. Dichotomies occur even in the upper parts of the pinnæ. In both species the pinnæ are entire, subalternate and closely-set on the upper side of the terete rachis, which thus appears almost entirely on the under side of the frond (Pl. 8. fig. 18). In most cases compression has been too great to allow of the subauriculate nature of the upper basal angle being distinguished, though the example figured shows it well (Pl. 8. fig. 5; *cf.* 4, Taf. 1, figs. 2 *a* & 3 *a*).

The abundance of *Ptilophyllum* fronds, particularly *P. cutchense*, in block I., indicates their possible connection with the stem represented (*cf.* Seward, 27, pp. 192–194, text-figs. 30 A & 32, a reference to a similar stem with *P. cutchense* leaves attached). There are, however, no indications of actual attachment in the material now under consideration.

Dictyozamites, Oldh.

Dictyozamites falcatus (Morris) nob.

Block II. shows many fragments of detached fronds referable to the genus *Dictyozamites*, Oldh. (Pl. 9, fig. 1 *a*; Pl. 8. fig. 6; *cf.* 8, pl. 2. figs. 5 & 6; 9, pls. 3, 4, 5; 4, Taf. 4. figs. 7 & 8; Tafs. 5 & 6; 19, pl. 24. figs. 1 & 2, *Dictyopteris falcata*). The pinnæ are alternate, varying somewhat with regard to size, shape, and form of apex, and are inserted by the middle only of the base, being sessile or slightly stalked. The basal angles are apparently subauriculate. The pinnæ are specially characterized by their numerous veins radiating from the base, dichotomising and anastomosing to form a reticulum, of which the central meshes are long and nearly parallel, while those towards the apex and margin are shorter. Morris terms leaves with similar pinnæ *Dictyopteris falcata*, believing them to be of filicinean affinities, but Oldham (19, p. 39) prefers to regard them as cycadean fronds. He accordingly substitutes the generic name *Dictyozamites*, retaining Morris's species. Feistmantel (4, pp. 18 & 19), considering *Dictyozamites* to be characteristic of the Rajmahal Group and purely Indian, distinguishes the type as *D. indicus*, but recent discoveries of exactly similar fronds in other parts of the world render it advisable to retain the former name *Dictyozamites falcatus* (see 16, 28, 41, 42).

Sections of rachises and pinnæ.—In the majority of cases, the rachises in section show no clear structure, though in some examples the vascular system is seen to be composed of separate strands arranged in a double series in the form of a U (Pl. 9. fig. 7; Pl. 7. fig. 13; *cf.* 34, pl. 62. fig. 1; pl. 63, fig. 1; and 37, p. 99, fig. 52), a disposition probably derived by the depression of the adaxial members of an original circular or elliptical system having the xylem directed inwards. Such a system is seen in the leaf-bases surrounding the cycadean stem in block I. (Pl. 9. fig. 8; Pl. 7. figs. 17 & 18; *cf.* 37,

p. 59, figs. 30 & 33). In vascular bundle arrangement, the present examples agree with the majority of Wieland's Cycadeoidean rachises, which, he points out, show a fern-like V-shaped or closed grouping of the bundles (37, p. 62), characteristic of "a pinnular bundle supply arising from the upper sides of the system" producing closely-set pinnules as in *Ptilophyllum* and *Otozamites*, while the omega type of bundle arrangement of most recent Cycads "results in a heavy continuous ridge between the two rows of pinnules" (p. 63).

Nothing can be determined from longitudinal sections with regard to the nature of the xylem elements; indeed, in most sections, longitudinal or transverse, it is difficult to distinguish any vascular tissue at all. Nor can the rachis sections be referred with certainty to either *Ptilophyllum* or *Dictyozamites*, except in one case where a transverse section showing the U-shaped vascular arrangement is definitely correlated with an impression of a *Ptilophyllum* leaf.

Where the attachment of the pinnæ with the rachis is seen in section, it is clear that in some cases the pinnæ are much more closely-set than in others; this condition probably corresponds with greater approximation of the arms of the vascular system, as some of the sections seem to suggest (Pl. 8. fig. 18 *a* & *b*). It appears possible from examination of the fronds on the surfaces of the blocks that the less closely set examples are *Dictyozamites*, but no essential difference of bundle arrangement can be detected.

In none of these cases of pinna-attachment is it possible to obtain a clear idea of the pinna structure. In an example of *Ptilophyllum cutchense* lying at the surface of block II., however, the structure, as far as can be determined, shows an upper small-celled epidermis, with possibly an upper hypoderm, palisade and spongy mesophyll with vascular bundles not showing structure, and a lower epidermis, well-marked but not sufficiently clear to show stomata (Pl. 8. fig. 4 *a* & *b*; see also Pl. 9. fig. 6). The pinnæ decrease in thickness somewhat abruptly towards the margin and appear pointed in transverse section. It is possible, however, that this is a variable character.

Other pinnæ present in the sections, though of essentially the same structure as those of *Ptilophyllum cutchense*, were evidently originally thinner in texture. Further, they possess relatively a greater number of vascular bundles, while the pinna-margins are decidedly rounded (Pl. 9. fig. 5). In the pinna of this type figured, each vascular bundle is seen to possess a small mass of xylem presumably centrifugal in nature; for adjacent to this xylem, above and below, are cavities representing, no doubt, centripetal xylem and protoxylem towards the upper surface of the leaf, and phloem towards the lower surface (Pl. 8. fig. 7). Pinnæ of this second type may be tentatively referred to *Dictyozamites falcatus*, since the external characters of this species suggest a closer correspondence with the structure as seen in section than do those of *Ptilophyllum acutifolium*.

There can be little doubt with regard to the cycadean affinities of these fronds. Both types are cycadean in general plan, agreeing with such recent Cycads as some of the Zamias, which show palisade mesophyll. In the possession of palisade tissue there is agreement with *Cycadeoidea ingens*, Ward (35, pl. 7. fig. 4).

The distribution of sclerenchyma in connection with the vascular bundles in *Ptilophyllum* and *Dictyozamites* is not clear, though there is evidently a much smaller amount than in the cycadeoidean type figured by Wieland. (With regard to the surface-features of the leaves, see Section II. "Methods.")

ii. *Fructifications.*

Williamsonian type.

Block II. shows a *Williamsonia*-like fructification referred by Feistmantel, as already mentioned, to *Williamsonia gigas*, Carruth., on account of the large number of bracts surrounding it (Pl. 7. fig. 2; *cf.* 4, Taf. 2, figs. 1, 2, & 3; Taf. 3, figs. 1*b* & 4). The specimen, although apparently poorly preserved, was sectioned longitudinally and transversely. The transverse section reveals a central mass of petrified tissue surrounded by the transverse sections of the bracts, between which and the central structure is matrix material (Pl. 7. fig. 3). The bracts show seven vascular bundles as in the case of the leaf-bases surrounding the stem to be described in the next sub-section. The bundles are embedded in a ground-mass, having a broad peripheral band of sub-epidermal sclerenchyma (see under "Stems" for further description). In places there are indications of hairs between the bracts enclosing the central structure; in this respect, and also in the structure of the bracts, there is agreement with a Williamsonian female fructification from the Upper Jurassic of Scotland, described by Prof. Seward at a meeting of the British Association, 1911. No indications of male organs can be detected in the Indian specimen. The central mass consists of cellular tissue, the arrangement of which is suggestive, in spite of its indefiniteness, of transverse sections of seed-stalks and interseminal scales, as shown by Wieland for *Cycadeoidea* (Pl. 9. fig. 10; *cf.* 36, pl. 8. fig. 6; pl. 10. figs. 14 & 16; and 37, p. 119, fig. 61). Owing to lack of structure at the edge of the central portion it is impossible to determine whether the transverse section was taken in or below the ovule-bearing region.

The longitudinal section of the fructification is useless from a structural point of view. In the extreme upper part of the central mass, however, the oiled cut surface corresponding to the longitudinal section shows the ends of its vertically-running constituents, the appearance being suggestive of the presence of interseminal scales and ovules (Pl. 7. figs. 4 & 5).

In spite of the meagre evidence afforded by this petrifaction, its similarity to Seward's *Williamsonia* is sufficient to support its reference to the "Williamsonian type" of fructification, this being regarded as of Bennettitalean affinities on account of the close correspondence to such forms as *Bennettites Gibsonianus*, Carruth.

Block II. shows the moulds of bract-like structures and the reverse of the bract-bases. Below these, and slightly to one side, is a raised mass, apparently of silicified wood, probably belonging to the axis which bore the bracts (Pl. 7. fig. 1). The arrangement of the whole structure suggests that it represents part of a bract-bearing fructification axis, referable to the Williamsonian type. The James Yates collection of

Yorkshire Williamsonias, in the Paris Museum *, contains several such axes, certain of which have been mentioned by Saporta (21, pl. 81. fig. 1), Seward (26, p. 276), and Wieland (38, p. 98; 39, p. 448, fig. 6). (For further references, see Seward, 27, p. 182; Saporta, 22, pl. 240 to pl. 243.)

iii. *Stems.*

Williamsonian type.

Block I. shows a portion of a cycadean stem (Pl. 9. fig. 4) 10·1 cms. in length and about 5 or 6 cms. in diameter. Part of the fragment shows the armour of leaf-bases with indications of ramental packing between them (Pl. 7. fig. 16), while part has the outer cortical parts broken away, exposing the stele. At the widest part of the stem is a scar (Pl. 9. fig. 4, *a*; Pl. 7. fig. 14), evidently of a lateral structure which has completely fallen away. Below it the wood is badly shattered, and it is impossible to discover how the branch was supplied with vascular elements. There are no indications as to the nature of this lateral branch which may have been vegetative or reproductive. The presence of bract-like structures surrounding the region of the scar (Pl. 7. figs. 14 & 15) suggests the possibility that it was left by a bract-bearing floral axis.

Owing to the absence of a large part of the armour, it is not possible to determine with certainty whether there are zones of large and small leaf-scars, though towards the lower end of the stem-fragment the few remaining scars are large, and longer than they are broad; while in the region of the scar they are small, and broader than long (Pl. 9. fig. 4). All the scars are, however, more or less rhomboidal to lozenge-shaped (19, p. 36).

In the lower part of the stem there is a large weathered leaf-base, showing seven slight depressions, representing the vascular bundles of the leaf-supply. The vascular bundles correspond in position to those of the leaf-base sections, there being two adaxial, three abaxial, and two more or less lateral (Pl. 7. fig. 17 *a* & *b*; *cf.* fig. 17 *c*, an example of a transversely broken leaf-base; also Pl. 9. fig. 8, a section of a leaf-base). The reverse of several leaf-bases, below the actual stem, shows the same occurrence of seven vascular bundles passing out to the leaf.

Cut surfaces and thin sections reveal the general structure of the stem and the leaf-bases (Pl. 8. figs. 8–15; Pl. 9. fig. 8). In transverse section, two or three series of leaf-bases are seen surrounding the stem. These possess an outer epidermis, a fairly broad peripheral layer of sclerenchyma, and an inner ground-mass of parenchyma with many secretory sacs. There are constantly seven vascular bundles arranged as in the diagram, the xylem being directed inward (Pl. 7. fig. 18; *cf.* arrangement in the weathered leaf-base). There is no indication of the expected mesarch structure of the vascular bundles, but it is probable that the protoxylem and centripetal xylem are not preserved, and that the mass of radially arranged elements seen in the most favourable cases is all

* Part of this collection has recently been acquired by Yale University.

centrifugal xylem; the phloem also is indistinguishable (Pl. 9. fig. 9). Between the leaf-bases are indications of ramental hairs (Pl. 7. fig. 18).

The cortex of the stem is fairly wide, and has many secretory sacs (Pl. 8. fig. 14). A tissue suggesting periderm is developed more or less irregularly in its inner layers (Pl. 8. figs. 10 & 13). Traces of leaf-supply strands are seen here and there (fig. 10), but it is impossible to obtain any idea as to their course. Phloem and cambium are not preserved. The wood is fairly compact, with numerous uniseriate medullary rays, and is of almost coniferous appearance (Pl. 8. figs. 9–12; *cf.* 27, p. 193; 37, p. 75, fig. 41). The xylem elements themselves are small and radially arranged. The radial longitudinal section of the upper part of the stem-fragment shows very occasional indications of tracheides with bordered pits arranged similarly to those of recent Cycads, as noted by Oldham and Morris (Pl. 8. fig. 15; see 19, p. 35). The wood, although much broken up, with a certain amount of separation into rings, appears to have been developed originally in a single continuous zone, the primary cambium having persisted. The breaking up of the xylem zone (Pl. 8. fig. 10) may have been occasioned by the conditions of preservation, or, as Oldham and Morris suggest (19, p. 35), by "the partial decomposition of the wood previously to its becoming mineralised." A similar appearance in an Indian cycadean stem is figured by Seward in his 'Catalogue of Mesozoic Plants' (27, p. 194, text-fig. 30 B).

The structure of the woody zone is undoubtedly endarch (Pl. 8. fig. 12; *cf.* 37, p. 75, fig. 41 *d*). The pith is parenchymatous with numerous secretory sacs, such as those in the medulla of *Cycadeoidea* (37, p. 77); there are no medullary vascular strands.

This stem possesses characters some of which are cycadeoidean, while others point to contact with the recent Cycads. The endarch nature of the xylem is common to all Cycadophyte stems, but the single compact woody zone with its narrow medullary rays is a characteristic feature of the cycadeoidean stems, wholly different from the looser structure of recent cycadean wood, formed in certain cases from successive cambiums. The Indian stem has multiseriately pitted tracheides similar to those of Cycads, as contrasted with the scalariform type usually occurring in the Cycadeoideæ (37, p. 75). Like these, however, it has numerous secretory sacs in its parenchymous ground-tissues, rather than the gum-canals of recent Cycads. So far as external characters are concerned, the stem described resembles that of a recent "armoured" Cycad in general appearance, for the leaf-bases, unlike those of the Cycadeoideæ, do not possess axillary structures; while in place of the ramental scales figured by Wieland (37) for his American Cycadeoideæ, and by Seward (25) for the English type *Cycadeoidea gigantea*, the leaf-bases are separated by a packing of ramental *hairs*.

In the structure of the xylem and medullary rays, and of the leaf-bases with their ramental hairs, the Indian stem agrees with the axis of Prof. Seward's Scottish *Williamsonia* fructification *. The leaf- and bract-bases in the two forms show exact correspondence in shape and size, in the amount of sclerenchyma and character of the ground-mass, and in the number and nature of the vascular bundles.

* Prof. Seward has now published a full account of this specimen (see Phil. Trans. Roy. Soc. ser. B, vol. 203, p. 101).

This agreement in structural details in the two specimens lends support to the reference of the stem to the Williamsonian type, a reference which is further strengthened by its association with fronds of *Ptilophyllum cutchense*, or, as Seward prefers to regard them, *Williamsonia pecten*. It will be remembered that fronds of this type are described in actual connection with a similar stem in the 'British Museum Catalogue of Mesozoic Plants' (27, p. 193).

The stem in block II. (Pl. 9. fig. 1; Pl. 8. figs. 16 & 17) is about 13·6 cms. long and 2·5 cms. wide, showing two complete zones of large leaf-scars and part of a third, and three zones of narrow scars. In the alternation of zones of large and small leaf-scars, its external characters agree with those of the Bucklandian type of stem (3). Some of the larger scars in their upper parts show five slight depressions marking the position of the vascular bundles which supplied the leaves (see Feistmantel, 7, p. 78). Lateral compression has occasioned the breaking up and displacement of much of the harder tissue, so that in section it is only possible to determine general characters. The pith and cortex are apparently of the usual type for this group, both having secretory sacs. In the cortex are several vascular structures, presumably leaf-trace bundles and irregularly developed periderm. The xylem, though now much broken up owing to conditions of preservation, shows signs of having formed one continuous zone, as appears to be usual in the fossil Cycadophyta (37, p. 74). It is compact with narrow medullary rays, and is clearly endarch (Pl. 8. fig. 16). No evidence with regard to the pitting of the elements is obtainable. In general characters this stem agrees with the previously described example, and is thus referred to the same comprehensive type.

C. Incertæ Sedis.

On the surface of Block IV. was noted a small rounded structure, which was carefully removed by chipping away a little of the surrounding matrix. The structure is evidently a small bilateral seed 3 mm. long, 3 mm. wide, and 2 mm. in thickness just above the base (Pl. 7. fig. 9). At the base there is an indication of a pedicel. It is impossible to determine whether the seed is Cycadean or Coniferous. Oldham and Morris (19, pl. 35. fig. 9) figure similar examples and incline (p. 36) to refer them to cycadean affinities, on grounds of association, although, as they point out, "so far as the seeds themselves are concerned, they might be coniferous."

IV. Conclusion.

The above investigation of certain gymnospermous types of Liassic age from the Rajmahal Hills in Bengal adds some facts as regards structural details to the already fairly extensive literature concerning Indian Mesozoic Plants (see references to the works of Feistmantel, 4–9; Oldham and Morris, 19). This literature, although dealing mainly with the external morphology of the types plainly indicates the similarity of the Mesozoic Flora of India to floras of the same age in other parts of the world. The geographical and geological distribution of the genera described above are too well known from the writings of various authors to render a discussion upon this subject

necessary or desirable. In this connection, reference may be made especially to the works of Prof. Seward on the Jurassic Flora (27, Introd. pp. 1–42; see also 28); of Dr. Wieland, whose 'American Fossil Cycads' includes an account of the geographical distribution of Mesozoic Cycadophyta (37, chap. i.); and of Feistmantel (6, pp. 47, 48), who remarks on the similarity of the Liassic and Inferior Oolite floras to be found along a tract running in a north-westerley direction from India to England. It is sufficient to note here that the anatomical evidence obtained from the present study of Indian fossils is in accordance with the accepted view of uniformity of the Mesozoic Floras.

V. Summary.

1. Certain gymnospermous types of Liassic age from the Rajmahal Hills in Bengal are described.

2. The cycadophyte remains present amongst the material show the association of stems and fructifications of Williamsonian type with foliage which may be considered as identical with the English fronds *Williamsonia pecten*. Portions of *Dictyozamites falcatus* fronds are also present. There are, however, no indications of actual attachment of leaves or fructifications with the stems.

3. The vegetative organs show a combination of recent and fossil cycadean characters. Externally the stems resemble those of recent "armoured" Cycads, the leaf-bases being separated by ramental hairs, instead of the scales usually found in the fossil forms. The single compact woody zone with its narrow medullary rays is a characteristic feature of the fossil stems, differing considerably from the looser structure of recent cycadean wood, formed in certain cases from successive cambiums. The Indian wood, however, shows multiseriately-pitted tracheides like those of recent Cycads, instead of the scalariform type usually occurring in the fossil stems. Like these, the parenchymatous ground-tissue has numerous secretory sacs rather than the gum-canals of the living forms. The "closed" arrangement of the vascular bundles of the leaf-bases and rachises is similar to that seen in the American fossil Cycads, as contrasted with the open or omega type of arrangement in most recent genera. Both types of frond are cycadean in general plan, agreeing with such living forms as some of the Zamias, which show palisade mesophyll, in the possession of which there is also agreement with *Cycadeoidea ingens*.

4. In the structure of the xylem and medullary rays, and of the leaf-bases with their ramental hairs, there is exact similarity between the Indian stems and the axis of Prof. Seward's Scottish *Williamsonia* fructification.

5. The Williamsonian fructification amongst the Indian types seems to agree, so far as evidence is available, in general characters and arrangement of parts with other Williamsonian and Bennettitean forms.

6. The structural evidence obtained, in conjunction with the external morphology of the specimens, supports the already accepted idea of a uniform Mesozoic Flora.

The writer desires to express gratitude to Prof. Seward for help and advice throughout the above investigations; also to Mr. H. H. Thomas for many useful hints with regard to methods of examination of the material.

References.

1. Ball, V.—The Geology of the Rajmahal Hills. Mem. Geol. Survey, vol. xiii. 1877.
2. Brongniart, A. Prodrome d'une histoire des végétaux fossiles. 1828.
3. Carruthers, W.—On Fossil Cycadean Stems from the Secondary Rocks of Britain. Trans. Linn. Soc. vol. xxvi. p. 675. 1870.
4. Feistmantel, O.—Ueber die Indischen Cycadeen Gattungen *Ptilophyllum*, Morr., und *Dictyozamites*, Oldh. Palæontologische Beiträge, i. 1876.
5. —— Fossil Flora of the Gondwana System. Jurassic (Oolitic) Flora of Kach. Mem. Geol. Survey of India, vol. ii. ser. xi. pt. i. 1876.
6. —— Ueber die Gattung *Williamsonia*, Carr., in Indien. Paläontologische Beiträge, ii. 1877.
7. —— Jurassic (Liassic) Flora of the Rajmahal Group in the Rajmahal Hills. Palæontologia Indica, vol. i. ser. 2, pt. ii. 1877.
8. —— Jurassic (Liassic) Flora of the Rajmahal Group from Golapili (near Ellore), S. Godavri District. *Ibid*, pt. iii. 1877.
9. —— Outliers of the Madras Coast. *Ibid.* pt. iv. 1879.
10. Fliche, P.—Contribution à la Flore Fossile de la Haute-Marne. Bull. de la Soc. des Sciences de Nancy. 1900.
11. Hollick, A., and Jeffrey, E. C.—Cretaceous Coniferous Remains. Memoirs of the New York Botanical Garden, vol. iii. 1909.
12. Knowlton, F. H.—The correct Technical Name for the Dragon Tree of the Kentish Rag. Geological Magazine, decade v. vol. viii. Oct. 1911.
13. Lindley, J., and Hutton, W. The Fossil Flora of Great Britain, vol. iii. 1835.
14. Mackie, S. J.—The Dragon Tree of the Kentish Rag. Geologist, vol. v. p. 401. 1862.
15. Medlicott, H. B., and Blanford, W. T.—A Manual of the Geology of India. 1879.
16. Nathorst, A. G. Sur la Présence du Genre *Dictyozamites*, Oldham, dans les Couches jurassiques de Bornholm. Overs. kongl. dansk. Vidensk. Selsk. Forhandl. p. 96. 1889.
17. —— Ueber die Anwendung von Kollodiumabdrücken bei der Untersuchung fossiler Pflanzen. Ark. för Botanik, vii. 1908.
18. Oldham, R. D. A Manual of the Geology of India. 1893. (A Revision of the Manual by Medlicott and Blanford, 1879.)
19. Oldham, T., and Morris, J. Fossil Flora of the Rajmahal Hills. Palæontologia Indica, vol. i. ser. 2, pt. i. 1862.
20. Phillips, J. Illustrations of the Geology of Yorkshire. 1829.
21. Saporta, Le Marquis de. Plantes Jurassiques. Paléontologie Française; T. ii. Cycadées. 1875.
22. —— *Ibid.* T. iv. Types Proangiospermiques, etc. 1891.
23. Seward, A. C. The Wealden Flora. Part II. Gymnospermæ. (Catalogue of Mesozoic Plants in the British Museum.) 1895.
24. —— Notes on the Geological History of Monocotyledons. Ann. of Bot. vol. x. p. 205. 1896.
25. —— On *Cycadeoidea gigantea*, a new Cycadean Stem from the Purbeck Beds of Portland. Quart. Journ. Geol. Soc. London, vol. liii. Feb. 1897.
26. —— On the Leaves of *Bennettites*. Proc. Camb. Phil. Soc. vol. ix. pt. v. Mar. 8, 1897.
27. —— The Jurassic Flora. Part I. Yorkshire. (Catalogue of Mesozoic Plants in the British Museum.) 1900.

28. Seward, A. C.—On the Occurrence of *Dictyozamites* in England, with Remarks on European and Eastern Mesozoic Floras. Quart. Journ. Geol. Soc. vol. lix. p. 217. May 1903.
29. —— Fossil Floras of Cape Colony. Annals of the South African Museum, vol. iv. pt. i. 1903.
30. —— The Jurassic Flora. Part II. (Catalogue of Mesozoic Plants in the British Museum.) 1904.
31. —— The Jurassic Flora of Sutherland. Trans. Roy. Soc. Edin. vol. xlvii. pt. iv. no. 23. 1911.
32. Stopes, M. C.—The Kentish Rag Dragon Tree. Geological Magazine, n. s., decade v. vol. viii. p. 55. Feb. 1911.
33. —— The Name of the Dragon Tree. *Ibid.* p. 468.
34. Ward, L. F.—Status of the Mesozoic Floras of the United States. United States Geological Survey, monograph 48, pt. II. (plates). 1905.
35. Wieland, G. R.—The Leaf Structure of Cycadeoideæ. A Study of some American Fossil Cycads, Pt. II. Amer. Journ. of Science, vol. vii. Apr. 1899.
36. —— The Female Fructification of *Cycadeoidea*. A Study of some American Fossil Cycads, Part III. *Ibid.*, May 1899.
37. —— American Fossil Cycads. Publication of the Carnegie Institute of Washington. 1906.
38. —— Historic Fossil Cycads. Amer. Journ. of Science, vol. xxv. 1908.
39. —— On the Williamsonian Tribe. *Ibid.* vol. xxxii. Dec. 1911.
40. Williamson, W. C.—Contributions towards the History of *Zamia gigas*. Trans. Linn. Soc. vol. xxvi. p. 663. 1870.
41. Yabe, H.—Mesozoic Plants from Korea. Journal of the College of Science, Imperial University of Tokyo, Japan, vol. xx. article 8. 1905.
42. Yokoyama, M.—Jurassic Plants from Kaya, Hida, and Echizen. *Ibid.* vol. iii. p. 1. 1890.

EXPLANATION OF THE PLATES.

Plate 7.

Fig. 1. Probable axis of fructification of Williamsonian type, shown on the surface of block IV. *a*, moulds of bracts; *b*, reverse of bract-bases; *c*, axis. Nat. size.

2. Williamsonian fructification of block II. Nat. size.

3. The same, in transverse section, showing also the matrix of the block. *a*, central part of fructification; *b*, surrounding bracts; *c*, a petiole in transverse section; *d*, a petiole in longitudinal section; *e*, pinnæ in transverse section; *f*, sections of coniferous twigs. Nat. size.

4. The same, in longitudinal section. *a*, central part of fructification; *b*, bracts; *c*, matrix; *d*, portion of the fructification shown in fig. 5. Nat. size.

5. *d*, of fig. 4, showing appearance suggestive of seeds and interseminal scales. × 6.

6. *Brachyphyllum mamillare*, portion of a leafy twig. × 3.

7. The same, in transverse section, showing the leaves surrounding the compressed central stem. × 20.

8. Coniferous wood; longitudinal section showing pitted tracheides. × 180.

9. Seeds of block IV. *a*, nat. size; *b* and *c*, two views of a seed showing bilateral symmetry; note indication of pedicel. × 4.

Fig. 10. Collodion-film taken from the under surface of a pinna of *Ptilophyllum cutchense*, indicating *a*, the elongated epidermal cells marking the course of a vein; and *b*, the shorter cells between the veins. × 110.

11. The same, indicating a probable stoma-opening, *a*, with its surrounding cells. × 350. (*Cf.* fig. 12.)

12. *Macrozamia corallipes*, a portion of the lower cuticle, showing a stoma-opening, *a*, and the surrounding cells. × 350. (For comparison with fig. 11.)

13. Diagrammatic representation of the petiole shown on Pl. 9. fig. 7. Note the arrangement of the bundles, outlining a U, with the xylem (shaded) directed inwards. × 20.

14. Scar of the stem shown on Pl. 9. fig. 4 (see *α*). *a*, moulds of bracts surrounding the scar (*cf.* fig. 15 *a*). Nat. size.

15. Longitudinal section through the block, immediately to the left of the scarred stem shown in fig. 14, showing *a*, the moulds of the bracts surrounding the scar; *b*, the transverse sections of the bracts; *c*, matrix with petiole and pinna sections. Nat. size.

16. Williamsonian stem of Block I., leaf-bases. Note the indications of a "packing" between the leaf-bases. Nat. size.

17. The same. *a* and *b*, two views of a large weathered leaf-base; *c*, a leaf-base in the matrix, broken transversely. Note in each case indications of the presence of seven vascular bundles, and *cf.* fig. 18 and Pl. 9. fig. 8. *a* and *b*, nat. size; *c*, × 6.

18. The same, showing, somewhat diagrammatically, transverse sections of leaf-bases with indications of ramental hairs separating them. × 4.

19. (?) Reverse of the outer layers of the *Coniferocaulon* stem shown on Pl. 9. fig. 2. Note the indications of wrinkling and of elliptical markings. Nat. size.

Plate 8.

Fig. 1. *Ptilophyllum cutchense*, a portion of the frond shown on Pl. 9. fig. 3 *a*. Note the *impressions* of the under surfaces of pinnæ and their scars of attachment on the rachis. × 2.

2. *P. cutchense* (see Pl. 9. fig. 3 *d*). Upper surface of pinnæ. × 2.

3. *P. cutchense*, a frond-apex. Nat. size.

4. *P. cutchense*. *a*, portion of a frond shown on the surface of a block, × 2; *b*, section of one of the pinnæ of *a*. × 50. (*Cf.* Pl. 9. fig. 6.)

5. *P. acutifolium*. Note indications of sub-auriculate nature of upper basal angle of pinnæ. × 2.

6. *Dictyozamites falcatus*, portion of frond, showing the attachment of the pinnæ and the reticulate venation. × 2.

7. Part of transverse section of the pinna also shown on Pl. 9. fig. 5. *a* and *b*, cavities left presumably by the non-preservation of the centripetal xylem and phloem respectively; *c*, supposed centrifugal xylem. × 100.

8. Part of transverse section of a leaf-base, showing *a*, epidermis; *b*, peripheral sclerenchymatous layer; *c*, ground-mass with secretory sacs; *d*, vascular bundle. × 50. (See Pl. 9. fig. 8.)

9. Transverse section of the Block I. Williamsonian stem taken about 1 cm. below scar (see Pl. 9. fig. 4, *x*). *a*, the leaf-bases surrounding the stem. Nat. size. Note that much of the cortex and xylem have fallen away from the stem.

10. Transverse section of the same stem taken at the level of *x'*, Pl. 9. fig. 4. Note apparent separation of the xylem into rings. *a*, cortex with secretory sacs; *b*, periderm; *c*, xylem; *d*, probable leaf-trace; *e*, pith; *f*, bending-out of woody cylinder in the region of the scar. Nat. size.

Fig. 11. Transverse section of the xylem of the Block I. stem. Note the uniseriate medullary rays. × 275.

12. Transverse section of the xylem, showing its endarch nature. *a*, the passing-out of a leaf-trace; *b*, the pith with secretory sacs. × 50.

13. Transverse section of the periderm-like tissue shown in position in fig. 10, *b*. × 50.

14. Transverse section of the ground-tissue of the Williamsonian stems, showing secretory sacs. × 50.

15. A tracheide of the Block I. stem, showing multiseriate fitting. × 350.

16. Transverse section of the Block II. Williamsonian stem (see Pl. 9. fig. 1). *a* and *b*, probable leaf-traces; *c*, leaf-base. × 3.

17. Section of part of Block II., showing *a*, longitudinal section of Williamsonian stem; *b*, oblique sections of coniferous wood; *c*, the petiole shown on Pl. 9. fig. 7. Nat. size.

18. Diagrammatic representation of two conditions of the petiolar vascular system; in *b* the arms of the U are slightly closer than in *a*, seeming to correspond to the closer setting of the pinnæ. × 20.

Plate 9.

Fig. 1. Williamsonian stem of Block II. Note the zones of large and small scars. *a*, *Dictyozamites falcatus*. Nat. size.

2. *Coniferocaulon* stem of Block III. Slightly reduced.

3. Fronds of Block I. *a*, *Ptilophyllum cutchense*; *b*, frond-apex; *c*, *P. acutifolium*; *d*, upper surface of *P. cutchense*. Nat. size.

4. Williamsonian stem of Block I. *α*, scar; *x* and *x'*, levels of sections figured on Pl. 8. figs. 9 & 10. Note slight variation in size of leaf-bases, seen at the right-hand side of the stem. Nat. size.

5. Transverse section of the pinna, a portion of which is shown on Pl. 8. fig. 7. × 20.

6. *P. cutchense*, transverse section of pinna (*cf.* Pl. 8. fig. 4, *b*). × 20.

7. Transverse section of a petiole showing arrangement of bundles (*cf.* Pl. 7. fig. 13). × 20.

8. Transverse section of a leaf-base. *α*, two vascular bundles shown in fig. 9 (*cf.* Pl. 7. figs. 17 & 18; Pl. 8. fig. 8). × 20.

9. Two vascular bundles shown at *α*, fig. 8. × 100.

10. Portion of transverse section of Williamsonian fructification. × 100.

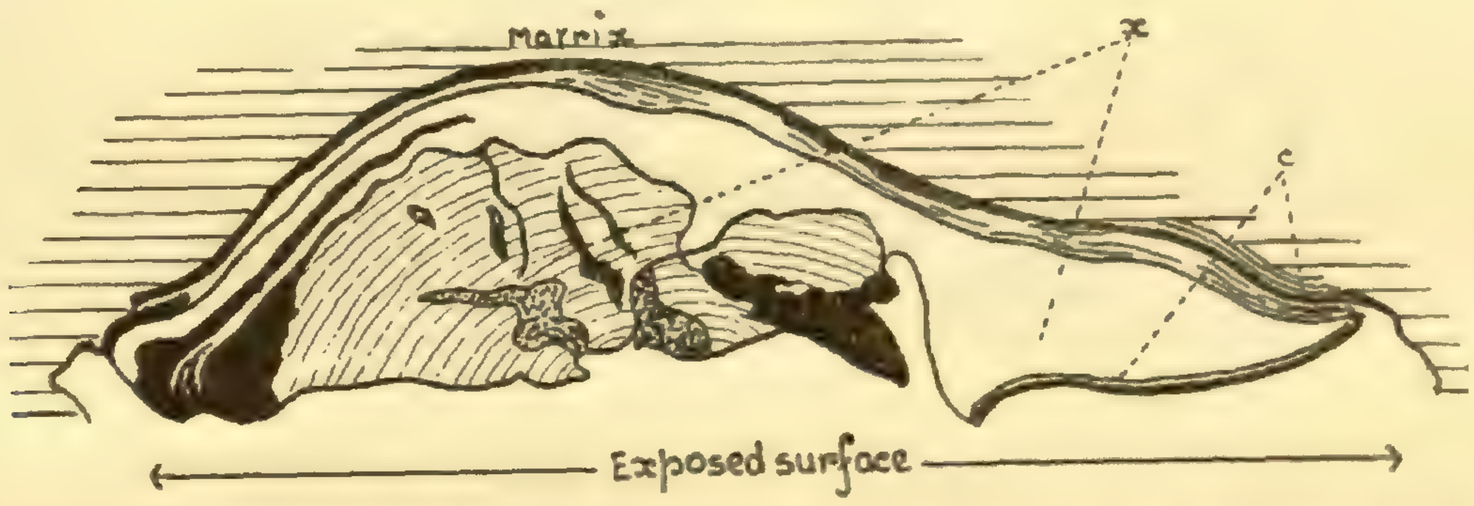
APPENDIX.

(Note on the Internal Structure of *Coniferocaulon* sp.)

Since the reading of the paper on "Some Indian Jurassic Gymnosperms," two sections, a longitudinal and a transverse, have been obtained from the block III. stem, *Coniferocaulon* sp. These shed very little light on the general structure of the specimen; the few facts that they contribute, however, serve to confirm the view that it represents the remains of a coniferous stem.

The transverse section passes through the stem below a lateral structure, evidently a branch-base*. It shows that the stem is much compressed and imperfectly preserved, the breaking up of the tissues being probably due in part to decay before petrifaction. The greater part of the preserved tissues consists of the woody axis of the plant (text-fig. 1, *x*). Partly surrounding this is a layered tissue, *c*. The thickness of this layer is much greater on the side of the stem protected by the matrix of the block than on the exposed surface, where it is very thin (text-fig. 1, *c*). This indicates that the wrinkled surface shown in Pl. 9. fig. 2 does not represent the true external layer of the stem, so that in the case of this specimen it is

Text-fig. 1.



Coniferocaulon sp.—Diagram of the transverse surface of the stem, showing the incomplete, imperfectly preserved woody axis *x*, with the surrounding layered tissues *c*. As the diagram indicates, the woody structure is not equally clear throughout the axis.

useless to compare the exposed surface with the external surface-features of *Zamia Skinneri* (according to Seward, 24, pl. xiv. figs. 1, 2, & 3) or with those of Araucarias of the Colymbæa section (according to Fliche, 10, p. 7). Dr. Stopes reaches the same conclusion in the case of a British Museum specimen (32, p. 56).

Neither the transverse nor the longitudinal section give any information concerning the nature of the protuberances present on the wrinkled exposed surfaces; it cannot be determined whether they have any connection with the vascular system or are merely cortical in origin. Dr. Stopes interprets similar protuberances in the case of some Cretaceous specimens of *Coniferocaulon* as being due to the presence of teredo-borings in the original structures (32, p. 55); but this explanation does not hold, apparently, in the present case.

On the cut transverse surface of the stem there are indications of zoning of the wood, though it cannot be determined whether the zones are seasonal or a result of petrifaction. In the transverse section the wood presents a "coniferous" appearance, the xylem elements being small, polygonal, and compactly arranged. The medullary rays seem to be uniseriate. In parts of the axis, structure is

---

* This lateral structure is not included in Pl. 9. fig. 2. Its position before sectioning was immediately above the shattered portion of the axis shown in the top left-hand corner of the photograph.

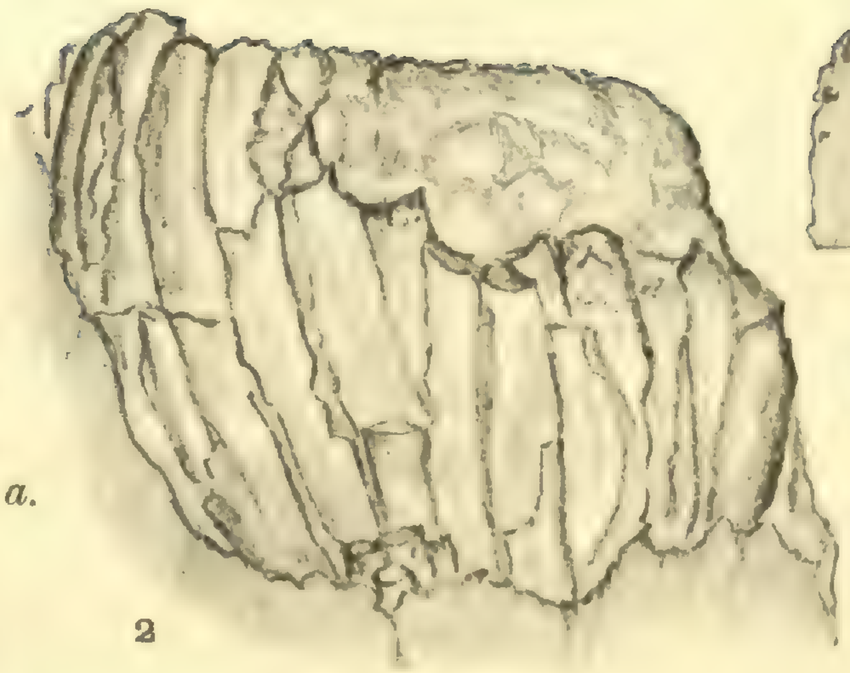
almost entirely obliterated, as seen in transverse section (those areas not marked by curved lines in the diagram); the woody nature of these areas is indicated by a comparison with the fractured vertical surfaces corresponding to them, these surfaces being regularly striated. The outer layered tissues show no definite structure; it is possible that they may originally have been corky in nature.

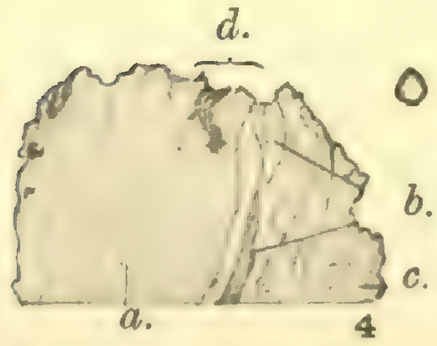
The longitudinal section passes through the lateral structure mentioned above, showing part of its axis in transverse section and part of the main axis in longitudinal section. The connection between this lateral structure and the main axis is obscure, owing to imperfect preservation and compression of the tissues. The longitudinal section of the wood shows a compact structure, but actual details are not clear. Nothing can be determined as to the appearance of the medullary rays in longitudinal section of the wood; and although occasionally there are indications that the tracheides may possess a single series of bordered pits, such as are shown in Dr. Stopes's figure (32, p. 57), preservation is not sufficiently good to allow of a definite statement being made on this point.

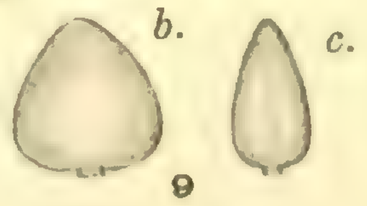
Although the general anatomical features of the stem cannot be determined, the coniferous appearance and texture of the wood is clear, and hence the reference of the specimen to *Coniferocaulon* is justified.

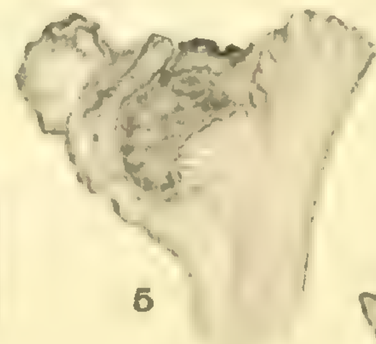
N. B.

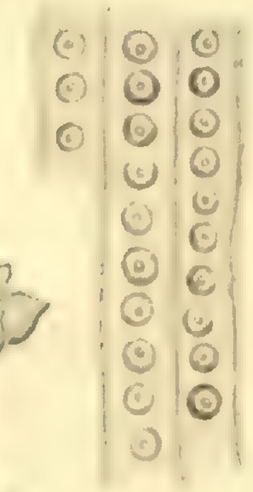
14*th February*, 1913.

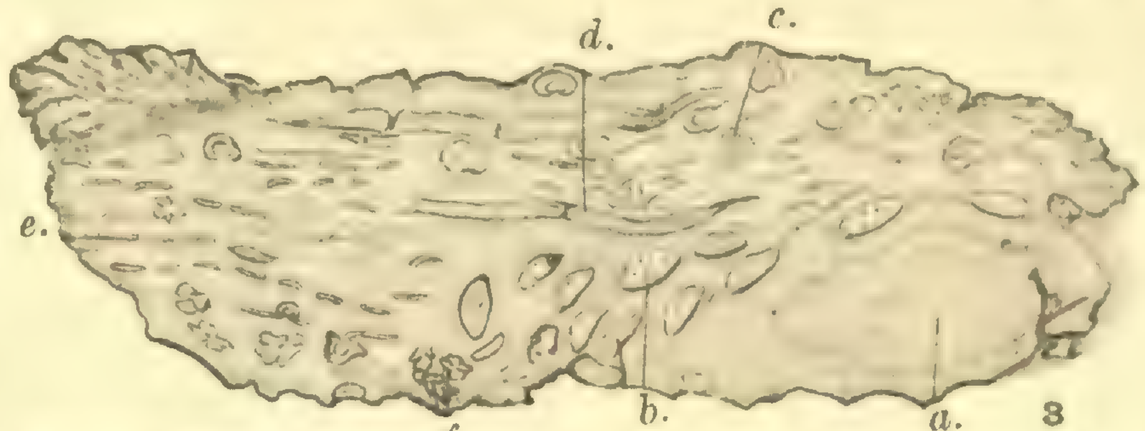


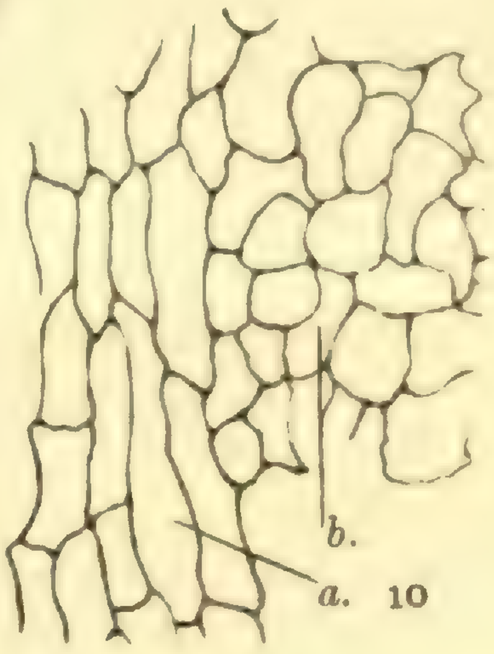


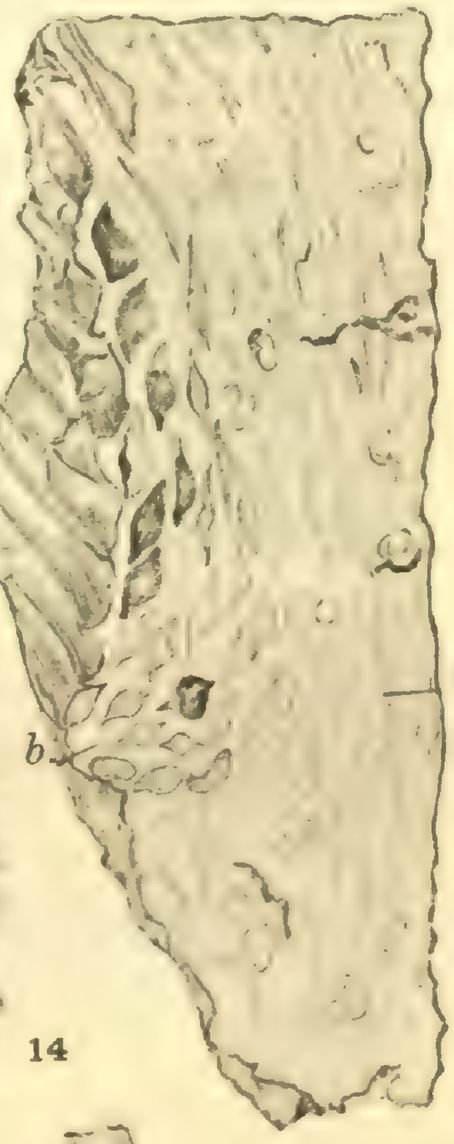


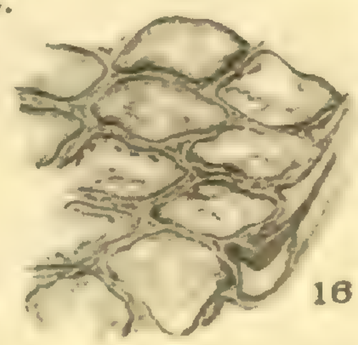


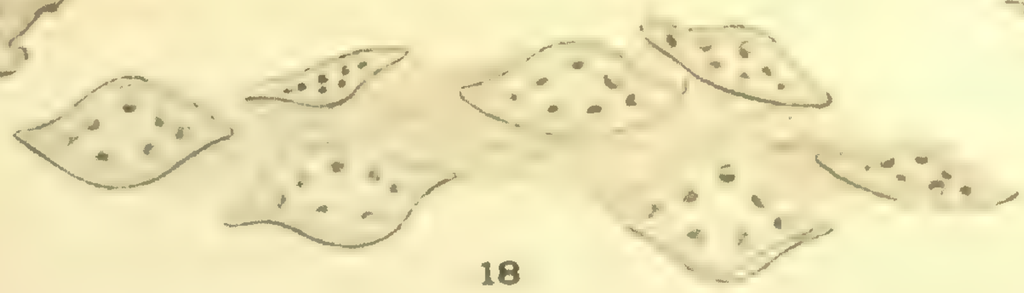












N.B. del.

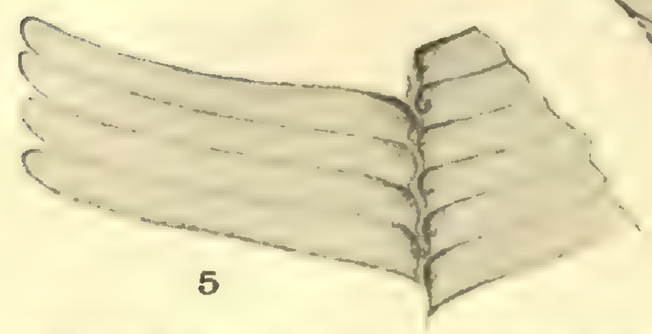
INDIAN JURASSIC GYMNOSPERMS.

1

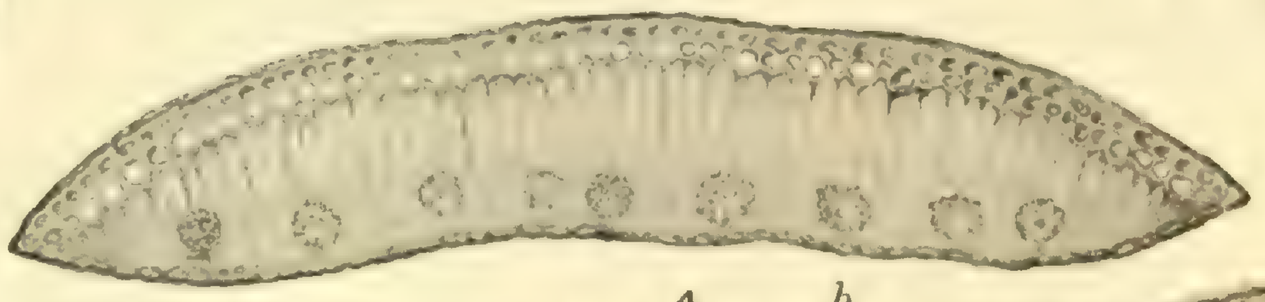
2

6

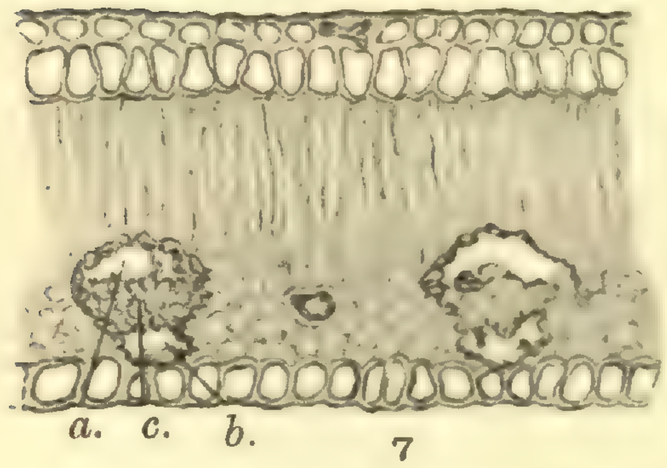
15



5



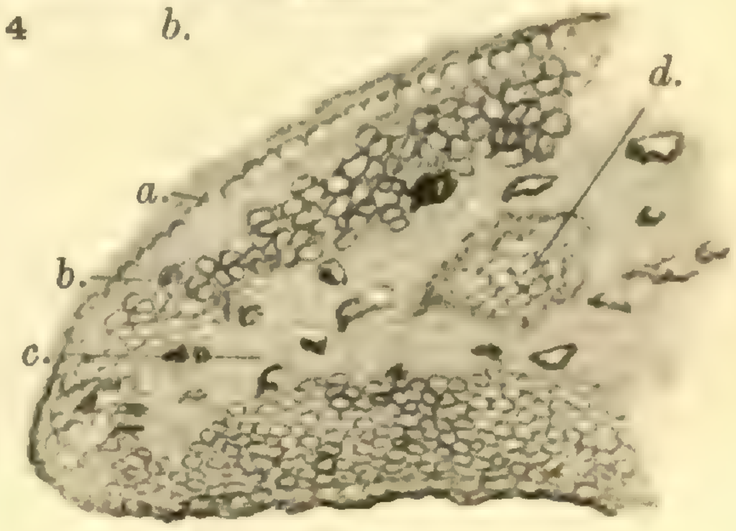
4 b.



a. c. b. 7

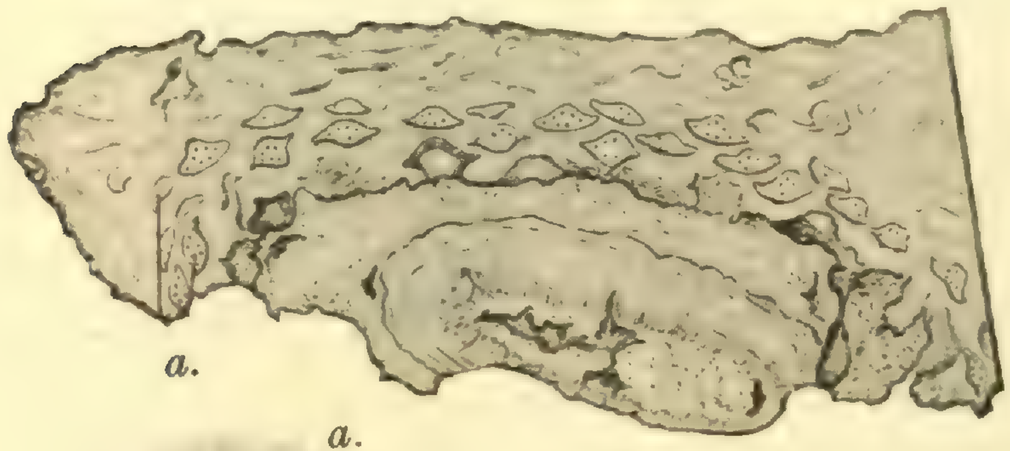
3

a.

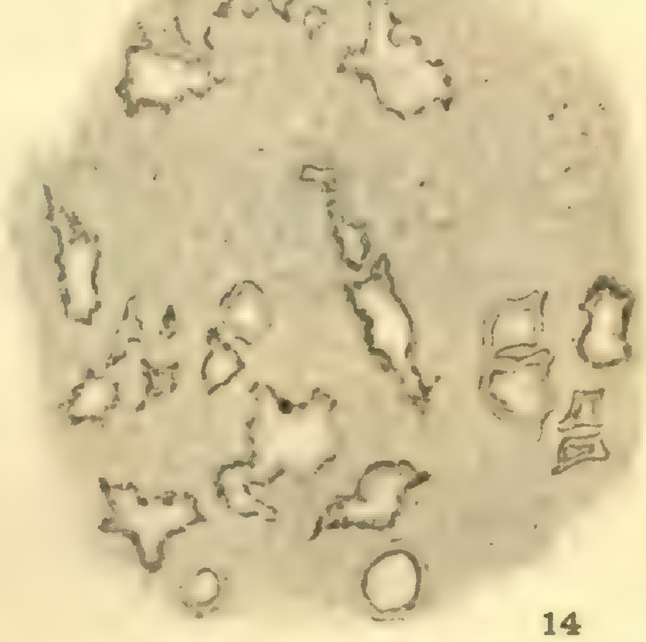


d. a. b. c. 8

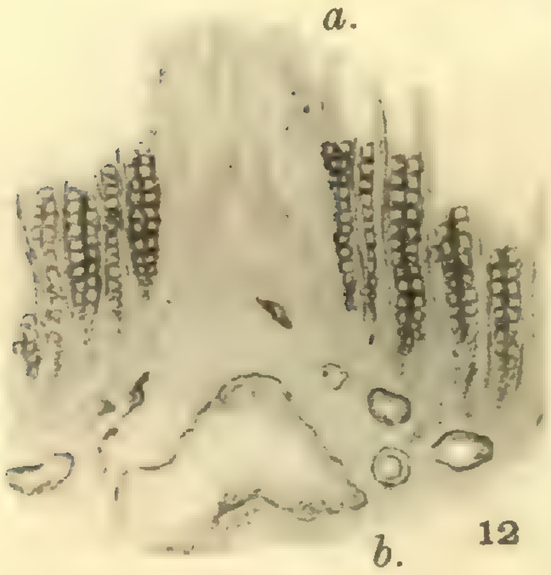
a. b. b. c. 17



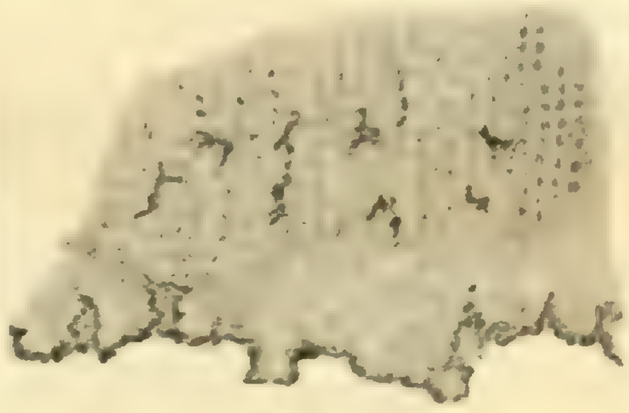
a. a. 9



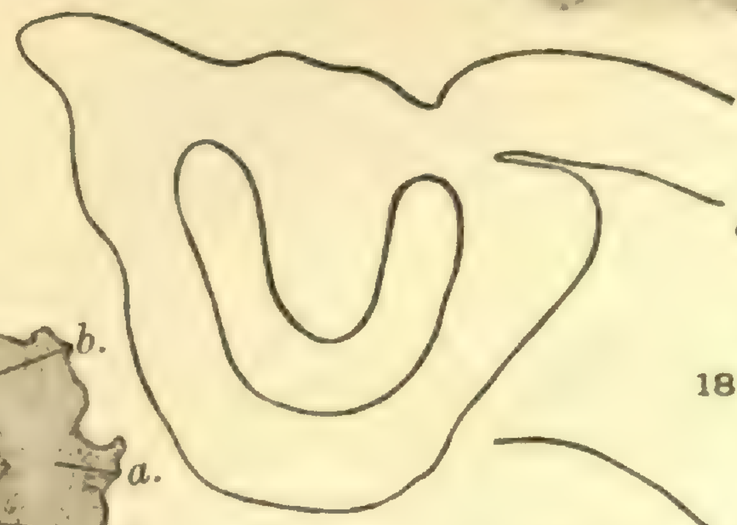
14



b. 12

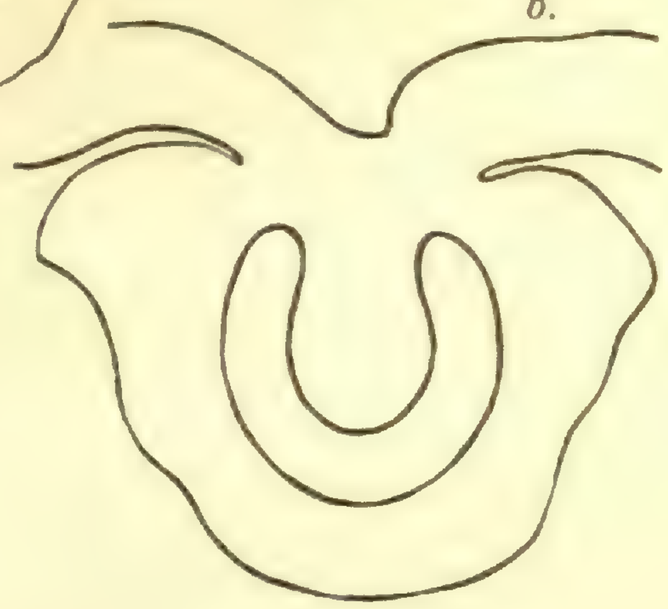


13

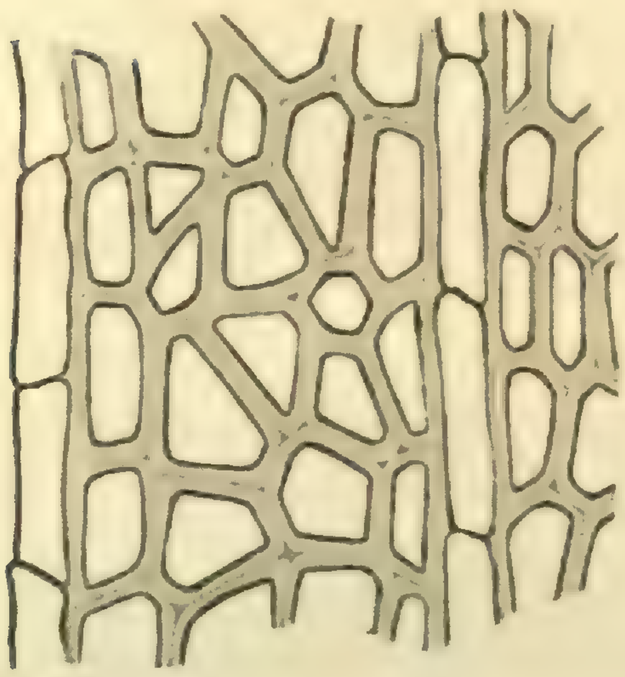


a. 18

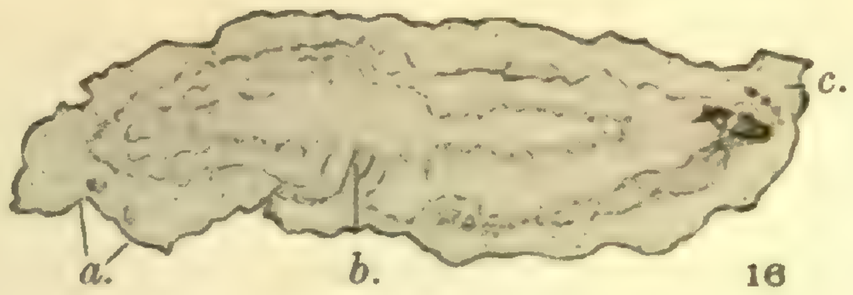
d. b. a. c. f. e. 10



b.



11

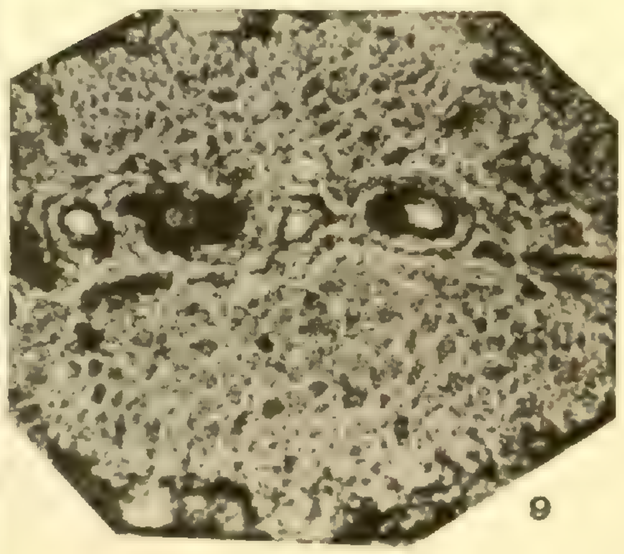


c. a. b. 16

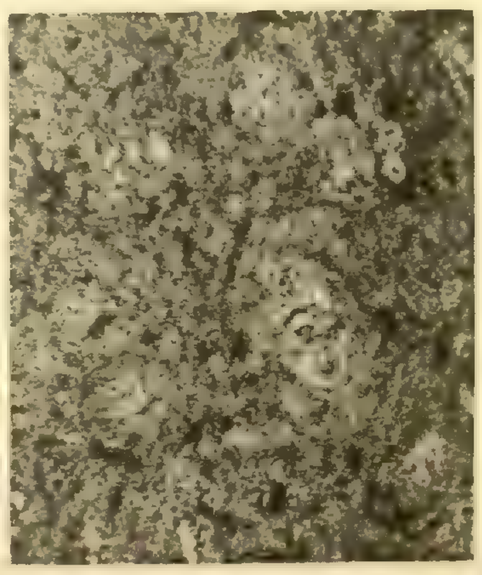
a.

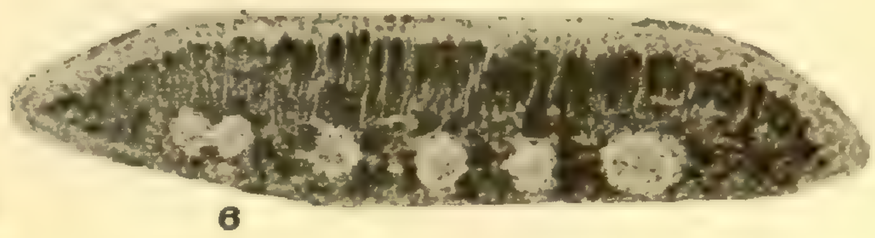
1

2


9

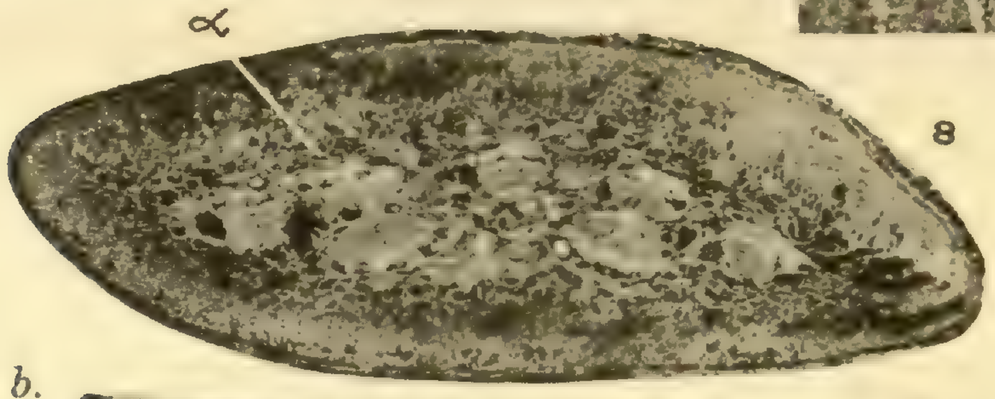
7


d


10

6

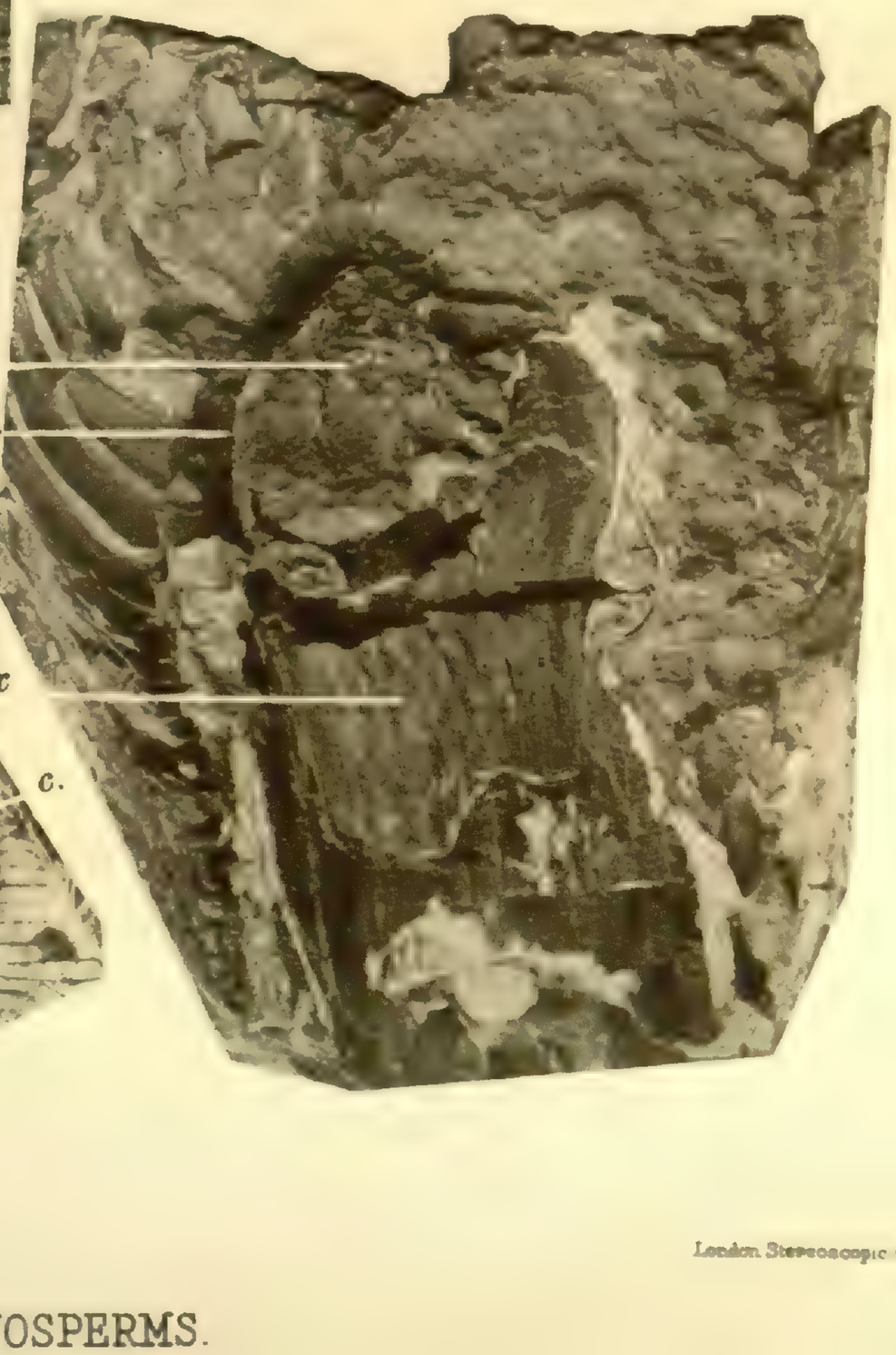
5


α

8

b.

a.


4

x^1

α

x

c.

3

d

W. Tams, Phot.

London Stereoscopic Co. imp

INDIAN JURASSIC GYMNOSPERMS.

III. Rhexoxylon africanum, *a new Medullosean Stem.*

By Nellie Bancroft, *B.Sc.(Lond.), F.L.S.*, 1851 *Research Scholar, Newnham College, Cambridge.*

(Plates 10 & 11.)

Read 6th February, 1913.

I. Introduction.

The specimen which forms the subject of this paper was sent to Prof. Seward by Dr. A. W. Rogers, the Director of the South African Geological Survey, as an unusual type of petrified stem-structure. The block was sent to Dr. Rogers without any information as to its locality or associations, but in his letter in reference to the fossil he writes:—"I have no doubt that the specimen came from the Cape." He adds: "It probably came from the Karroo rocks."

Since the Karroo Series ranges from the Dwyka boulder-beds and shales to the Stormberg Series—*i. e.*, in terms of European geological chronology, from the Upper Carboniferous (approximately) to the Rhætic or Lower Jurassic (5, pp. 233–243)—the exact age of the specimen must be left in doubt, so far as concerns evidence other than that supplied by the structural features themselves.

II. Description of the Specimen.

(a) *External Characters.*

The specimen is silicified, and represents what is evidently a portion of a stem, the outer layers of which are absent. The length of the specimen before cutting was about 6·5 cm. and the diameters 7·2×5·7 cm., the structure being somewhat elliptical in transverse section (Pl. 10. fig. 1; Pl. 11. fig. 8).

Externally the fossil has an irregularly ribbed appearance, with vertical and alternating bands of varying width and of two different textures. The more outstanding bands consist apparently of a fairly porous and loose ground-tissue, while the alternate bands show fine vertical striations and are very compact (Pl. 11. fig. 1, *a* & *st*). These correspond to the irregular masses of compact texture which are seen on the transverse surface of the stem (Pl. 10. fig. 12), and which are evidently vascular structures.

The cut transverse surface shows general ground-tissue, more compact towards the interior of the stem than at the outer parts, where here and there it is very porous (Pl. 11. fig. 8). Embedded in this ground-tissue, mainly at the periphery of the block, are the masses of compact tissue mentioned above. Each of these is presumably a stele

or part of a stele, and each of the complete steles is more or less heavily outlined by a dark brown coloration of the adjacent tissues (Pl. 11. figs. 3, 7, & 8).

Since it is impossible to know how much of the outer layers of the stem is lacking, the precise arrangement of the "steles"* must remain undetermined, although apparently one or more series were originally arranged peripherally. In addition to these, the central ground-tissue contains irregular isolated patches of tissue of the same compact structure and of varying size and shape. Situated near two steles belonging to what is considered as the inner series is an irregularly arched mass of the same tissue, consisting of two distinct parts (Pl. 10. figs. 1, 8, 9, & 11; Pl. 11. figs. 7 & 8).

A comparison of the cut and rough transverse sections of the block considered in connection with the outer surface-features shows that the masses of compact tissue run fairly regularly through the short length of stem without changing their position to any great extent, hence apparently without much branching or anastomosing. The cut vertical surface figured (Pl. 10. fig. 13) shows the straight and independent course of two of the steles. The irregular arched mass mentioned above slightly changes its relative position with regard to the members of the inner series of steles.

(b) *Internal Structure.*

Several transverse sections were cut from one end of the block, one of them being practically complete. This will be referred to as Section A. Three incomplete sections were taken from the same original thick section as this, and are therefore in approximately the same plane. These, with another incomplete transverse section, cut about a centimetre higher, do not reveal any facts as to change of position, branching, or anastomosing of the steles. An almost complete section (referred to as Section B) cut from the other end of the block, its position being about 4 cm. below the first complete section, shows no change in general arrangement of the steles, and very little change in their individual outlines. The central arched mass is more irregular and broken up; while one of the steles of the inner series (stele 5; see Pl. 10. figs. 3 & 10; Pl. 11. figs. 7 & 8) assumes a different form, possibly in relation to the separation of a trace. It also moves slightly away from stele 4 towards stele 6 in passing from the level of Section A to that of Section B. All the sections give the same details of structure.

Section A, corresponding approximately to the cut surface of the block shown in diagram (*cf.* Pl. 10. fig. 1 and Pl. 11. fig. 8), shows eight complete steles (1–8) embedded in the ground-mass, one almost entire (9), and parts of four others (10–13), all belonging to what is termed the "inner series." In addition to these there are seven groups of vascular tissues (*a*–*g*), evidently parts of steles which are not completely represented. These seem to belong to an outer series. Here and there amongst the steles, and more or less in connection with them, particularly in the case of the inner series, are groups of xylem elements, possibly representing a leaf-supply system (Pl. 10. fig. 1; Pl. 11. figs. 3, 7, & 8). Finally, in the central ground-tissue are patches of vascular elements

* The term "stele" is used provisionally for convenience in describing the structure of the stem. See footnote to p. 48 of Dr. Scott's monograph on *Sutcliffia insignis*.

varying in size and form. In this central system is included the irregularly arched group of vascular elements mentioned above, the group as a whole consisting of two *distinct* parts separated by a thin line of ground-tissue. In the description of the individual masses of vascular tissue this will be referred to as the "central stele."

Pl. 11. fig. 7, a photograph of Section B from the opposite end of the block, shows the steles lettered and numbered as in Pl. 11. fig. 8 and Pl. 10. fig. 1.

Structure of the Ground-tissue.

Silicification has rendered the material so homogeneous and transparent that it is impossible to determine definitely the structure of the ground-tissue in which the steles are embedded. It seems, however, to have been composed of moderately large parenchymatous cells, not generally very compactly arranged, though the apparent loose structure is probably to some extent due to the shrinking together of the cells and the consequent production of large spaces. A similar process is described by Weber and Sterzel for *Medullosa* (13, p. 74). As before mentioned, the ground-tissue at the periphery of the block appears more porous than at the centre. This may be due to more marked shrinking and destruction of the cells in the outer tissues.

In the curve of the central "stele" is an irregularly oval mass of fairly compact ground-tissue surrounded by a band of varying width of what appears to be periderm (Pl. 10. figs. 1, 8, 9, & 11; Pl. 11. figs. 7 & 8). Here and there the cells of the band are seen to be tabular in transverse section and radially arranged (Pl. 11. fig. 6). The mass of tissue enclosed by the band of periderm varies in area at different levels, according apparently to the variation of the curve of the central stele (*cf.* Pl. 11. figs. 7 & 8; also Pl. 10. figs. 1, 8, 9, & 11). Other more or less circular or irregular bands occur here and there, as shown in Pl. 11. figs. 7 & 8, *pd*.

In Section B the band of periderm encloses a mass of ground-tissue containing scattered and erratic xylem elements; some of these are cut obliquely, some transversely, but the majority are seen in longitudinal section (Pl. 10. fig. 11, xy^b). The band of periderm itself encloses here and there patches of xylem elements transversely cut. There is no trace of accompanying phloem (Pl. 11. fig. 6, xy^a). A similar enclosure of xylem elements by periderm is figured by Dr. de Fraine (1, p. 1050, text-fig. 16) in the case of two leaf-trace bundles in a stem of *Sutcliffia*. The author suggests that the abnormal condition may be due to injury perhaps by fungal growth. It is difficult to account for the formation of xylem enclosed by periderm in the present case. In the parenchymatous ground-mass are occasional groups of sclerotic cells, these occurring particularly in the neighbourhood of the steles (Pl. 10. figs. 3, 7, 10, & 16; Pl. 11. fig. 4). There is no certain evidence as to the presence of secretory cells or gum-canals, although here and there are cells with dark contents which may possibly represent secretory elements.

Briefly, then, the ground-tissue consists, as far as may be determined, of large-celled parenchyma, with sclerotic nests and bands of periderm in the neighbourhood of some of the steles.

Structure of the Steles.

These are irregular in nature, in some respects recalling the plate-rings of certain Medulloseæ. The stele 3 of the inner series, as seen in Section A, is a fairly typical example (Pl. 10. fig. 2; Pl. 11. fig. 3). At first sight, the impression is given of a somewhat elliptical mass or bundle, apparently a single complete structure. On closer examination, however, this is seen to consist of two closely-developed though *distinct* parts, the inner being much larger than the outer. These are presumably the product of two cambiums, one giving rise to normally, the other to inversely, orientated elements. The fact that the outer and inner, or normal and inverse, parts are independent structures is demonstrated by a slight space between them, and by the lateral discontinuity of the brownish elements, which are considered to represent crushed cambium and phloem (Pl. 10. fig. 2). The crushed tissue between the two masses shows here and there traces of vascular elements, and may represent a much reduced "partial pith" such as shown definitely in *Medullosa stellata*, Cotta, or *M. porosa*, Cotta (13, Taf. vii. figs. 1 & 4; p. 64, fig. 9), or it may represent ordinary ground-tissue with transfusion-cells, such as occurs in *Cycas*, between the normal and inverse bundles of the stem. On to this tissue abut what appear to be the protoxylems of the two masses (Pl. 10. figs. 2 & 15). The inverse group shows a lateral projection, probably a leaf-trace about to separate. The direction of the xylem elements is here slightly oblique (Pl. 10. fig. 2, *ob*; Pl. 11. fig. 3). In the diagram the dark line marking the external borders of the xylem represents the brown crushed cells, probably the remains of cambium and phloem. In the case of stele 3 nothing could be determined with regard to the form and arrangement of these cells. In Section B stele 3 shows very little change in form and structure; a slight interruption in the continuity of the radial series of elements appears in the inverse part, which is larger in proportion to the whole stele than in Section A (Pl. 11. fig. 7, *cf.* fig. 8).

A structure such as stele 3 may be compared with the plate-rings of *Medullosa stellata*, Cotta, which, it will be remembered, consist of a "partial pith" surrounded by secondary vascular tissues. In stele 3 the partial pith may be regarded as either much reduced in amount or crushed by subsequent secondary growth; while the lateral portions of the complete ring may have remained undeveloped by discontinuity of the cambium at these points. In this way a stele, consisting apparently of two distinct parts, may be derived from a complete ring of the *Medullosa stellata* type. Worsdell (14) considers that the so-called anomalous vascular structures in *Cycas* may be derived from Medullosean steles by local suppression of cambiums*, and the type of structure possessed by this South African stem may also have been produced in the same manner. Weber and Sterzel's figures (13, Taf. viii. fig. 3; Taf. iii. fig. 5) of *M. Solmsii*, Schenk, indicate a similar condition in some of the steles of that form, partial pith being reduced or practically absent, while there is also a smaller lateral development of the secondary tissues of the rings.

* See also Chodat ("Les Ptéridopsides des temps paléozoiques; étude critique," Arch. des Sci. phys. et nat. t. xxvi. 1908) and Matte ('Recherches sur l'appareil libéro-ligneux des Cycadacées': Caen, 1904) on this point.

Stele 4 (Pl. **10**. fig. 3; Pl. **11**. fig. 8) in Section A shows a very irregular type of development. Smaller normal and larger inverse parts (α and β) are present as before, but at one side these are so closely in contact as to appear almost continuous, the lateral break being less evident than in the case of stele 3. At the opposite side, however, the break is marked (Pl. **10**. fig. 3). The position and arrangement of the xylem elements marked γ suggest that they belong to β, the inverse xylem; the apparent separation may be due to a break in cambial activity, such as mentioned by Dr. Scott for *Medullosa anglica* (7, p. 90). At the side of the inversely developed xylem is a small group of obliquely running elements, possibly a leaf-trace. The crushed tissue external to stele 4 shows no trace of structure; while between the normal and inverse parts, which, as the diagram shows (Pl. **10**. fig. 3), are very closely in contact, the tissue is obliterated.

In Section B (Pl. **11**. fig. 7) stele 4 still shows the break in the development of the inverse xylem. The inverse and normal parts show no distinct separation laterally, the elements swinging round and appearing oblique and confused.

Stele 5 (Pl. **10**. fig. 3; Pl. **11**. fig. 8) presents in Section A the same arrangement of normally and inversely developed elements, the product of two independent cambiums. The inverse group apparently consists of two parts, β and γ; the continuity of the medullary rays at one point, however, suggests that β and γ are not really independent, although the arrangement of the xylem elements shows evidences of a slight disturbance. At the other side, however, there is a distinct break in the continuity of the medullary rays and of the radial series of elements, owing perhaps to a change of direction of the cambium at that point, or to a temporary cessation of cambial activity. At the left-hand side, the inverse group shows a separating trace; and at the right, further towards the periphery of the stem, is a separate trace, of interest on account of a few well-preserved cells in the crushed tissue accompanying it on its external border. These cells have delicate walls, and show evidences of having been arranged originally in a radiating series. Their nature and position suggest that they are phloem-cells. Traces of similar cells occur in the crushed tissue in connection with the outer normal part of stele 5. No partial pith is present between the closely-developed normal and inverse parts of the stele. In section B, stele 5 (Pl. **11**. fig. 7; Pl. **10**. fig. 10) shows a considerable amount of change in form and structure. The normal part is much reduced and, like the inverse, shows discontinuity of development. The elements of both groups are more or less oblique in section. The inverse part shows a large limb, possibly a trace, bending round towards the partial stele *d*, the direction of the elements being usually oblique. On the inner edge of the limb, closely approximating partial stele *d*, the elements run horizontally and show spiral thickenings on their walls. They are evidently the protoxylem of the limb.

Stele 6, which in Section A shows a structure very similar to that of stele 3 (Pl. **10**. fig. 4; Pl. **11**. fig. 8), is considerably changed in form at the level of Section B (Pl. **10**. fig. 10; Pl. **11**. fig. 7). The inverse part shows the break in development as before, and at the left-hand side (towards stele 5) is a large, much broken-up limb or trace with scattered sclerotic nests between the groups of xylem elements. This trace approaches

the normal part of stele 5 very closely. It is impossible to say whether the two steles 5 and 6 are really distinct, for the appearances almost suggest an anastomosis between them. In stele 6, as in 5, the elements are mostly oblique in direction.

Stele 7 is more suggestive of a complete stele than any of the others shown in Section A. The break in continuity of development at the left-hand side is very slight, the chief evidence of it being a confusion of direction of the xylem elements here (Pl. 10. fig. 5). It seems as if the outer and inner cambiums had almost joined at this point. At the right-hand side, however, where a trace is evidently about to separate from the inner mass, separation of the normal and inverse parts is very distinct. As usual, the structure of the tissues external to the xylem and between the two groups is obliterated. The transverse section from the opposite end of the stem-fragment includes only a small portion of this stele; its straight course, indicating but slight change of position or form, is shown by the vertical cut surface figured in Pl. 10. fig. 13.

The other steles of the inner series, as shown in Section A, do not present any new points of structure (see diagrams of steles 8 and 9, Pl. 10. figs. 6 & 7). In Section B, stele 9 shows the same outlines as in the first, 7 and 8 are incompletely represented, but their straight course and unbroken contours are shown in the diagram (Pl. 10. fig. 13). The position of steles 6, 7, 8, 9, and 10 in Section B appears slightly closed in towards the interior of the stem as compared with their position in Section A (*cf.* Pl. 11. figs. 7 & 8). Stele 10 is complete in Section B. It is much smaller than the others, consisting of a comparatively large, fan-shaped, inversely orientated part and a very small normal part. There is a slight indication of a partial pith, and both parts of the stele possess much of the brown phloem-like tissue (Pl. 11. figs. 7 & 4).

Immediately external to the inner steles, at the periphery of the stem-fragment, are several portions of large masses of normally orientated xylem (Pl. 10. fig. 1; Pl. 11. figs. 7 & 8, *a–g*), representing presumably a second series of steles. They are evidently the product of independent cambiums, which, so far as can be judged from the form of the incomplete masses, must have had a more or less arched course, as in the case of the cambiums of the inner series of steles. The first-formed xylem elements of these masses are sometimes almost in contact with the inner steles; in every case the ground-tissue between the two series of vascular structures is crushed.

The members of the second series of xylem groups correspond to the small parts of the inner ring, having no inversely orientated groups pairing with them. They are thus, in terms of the inner series, "partial steles." Partial steles *c*, *d*, and *e*, as seen in Section A, show breaks in the xylem, the medullary rays and radial series of elements being discontinuous along certain lines, although the general direction of development remains the same after the break as before (Pl. 10. fig. 3). This indicates a cessation of cambial activity for a time; or a new cambium may actually have arisen.

In association with the majority of these partial steles are patches and strands of xylem elements. In the case of *b* a large strand is seen in actual connection; but their nature, and in most cases their origin also, is extremely problematical. They may be developed by abnormal extensions of the cambium, or they may be ultimately connected

with the leaf-supply, although nothing could be decided on this point owing to the absence of the external layers of stem.

It is interesting to note that the direction of the xylem elements in these strands is very varied, for though the main masses in transverse section usually show transverse sections of the individual elements, the elements of the strands often run obliquely or horizontally, owing possibly to the extreme abnormality of the cambial growth (Pl. 10. figs. 3 & 10). Crushed tissue occurs with some of the lateral strands, showing occasionally thin-walled radially arranged cells, as in the case of some of the inner steles. Portions of partial steles *a*, *b*, *c*, and *d* are shown in Section B (Pl. 11. fig. 7). *a*, *b*, and *c* present practically the same appearance as in Section A. Partial stele *d*, however, shows great irregularity in structure (Pl. 10. fig. 10). The xylem is much broken up and the direction of the individual elements frequently varies from vertical to horizontal within a small area. The appearances suggest that the stem has been locally injured, causing abnormality in the development of the neighbouring tissue. In one place a band of periderm-like tissue borders the outer margin of the main mass of xylem (Pl. 10. fig. 10, *pd.*). Preservation is not sufficiently good to give any idea as to the formation of this tissue. It may be of the same nature as that described by Holden for *Myeloxylon* (3, p. 253). External to this is a band of badly preserved ground-tissue with sclerotic nests (*s*) and an isolated group of inversely orientated vacular elements (*vb*). Beyond this is a group of irregular xylem elements, apparently inversely developed, for a band of brown crushed tissue showing here and there traces of radial arragement appears on the *inner* edge of the group. The rest of the tissues of the partial stele are mostly oblique and show occasional breaks in development. A large trace appears at the left-hand side separated from the "trace" of stele 5 by a band of sclerotic nests. In the ground-tissue between the normal part of stele 5 and partial stele *d* are sclerotic cells and groups of variously orientated xylem elements accompanied by crushed tissue.

Other Vascular Structures of the Stem.

The central arched stele in Section A consists of two parts separated by rather more of the crushed and structureless tissue than occurs in the case of the inner steles (Pl. 10. fig. 8). The larger part of the stele shows a change from vertically running elements at one extremity to horizontal elements in the thin elongated limb at the other. This limb swings round in a hook-like manner, the elements maintaining their horizontal course. In the smaller part of the stele (that towards the centre of the stem) the elements are more or less oblique in direction throughout. The crushed tissue considered as representing phloem outlines the external margins of the two parts. In the thin hooked limb of the larger, where the elements run horizontally, this tissue becomes twisted from the inner side of the hook to the outer side (Pl. 10. fig. 8).

In one of the incomplete sections, slightly *above* the level of the complete Section A, only a trace of this hook is to be seen (Pl. 10. fig. 9); while no trace of it appears on the cut surface of the block, which is slightly *below* the level of the section (Pl. 10. fig. 1). Nor does the hook occur at the level of the section taken from the opposite end of the

stem-fragment, although there is a slight swinging round of the elements (Pl. 10. fig. 11). The break indicated in the smaller part of the stele in the complete Section A becomes more marked in passing through the stem to the opposite end of the block (*cf.* Pl. 10. figs. 8, 1, & 11). A break also appears in the larger portion of the stele. At the level of Section B the elongated limb beyond the break is fairly strongly marked, the xylem elements running more or less horizontally throughout its length. In the main part of the stele the xylem elements are oblique (Pl. 10. fig. 11).

The appearance of the central stele at the different levels indicates a probable sinuous and irregular course in a vertical direction.

It is interesting to note that opposite the ends of the central stele there are larger spaces than usual between the steles of the inner series; this is seen particularly in Section A (Pl. 11. fig. 8; Pl. 10. fig. 1). Whether or not it has any significance connected with the separation of traces from the central stele cannot be determined. Besides this structure the central ground-mass, particularly at the level of Section B, contains small isolated patches of xylem and crushed phloem arranged collaterally (Pl. 11. figs. 7 & 8) *. The course of the constituent elements varies from vertical to horizontal, the variation owing, no doubt, to the abnormality of cambial formation and growth indicated throughout the whole vascular system of the stem. It is difficult to estimate the significance of these bundles; they may be the remnants of a cauline vascular system, representing the "star-rings" of some Medulloseæ.

Structural Details.

In all the transverse sections the wood is seen to be compact and coniferous in type, resembling that of Cordaitean and Araucarian stems (Pl. 11. figs. 3 & 4). The steles and partial steles consist of radiating rows of tracheides, with uniseriate medullary rays, both primary and secondary, occurring at intervals. The number of rows of tracheides between the medullary rays varies from three to eight or nine. The tracheides are closely arranged and polygonal in shape; the lumen of each element is filled with layered siliceous material, this being less compact towards the centre (Pl. 10. figs. 14 & 15). In one or two cases the middle lamella may be seen (Pl. 10. fig. 14, *ml*).

The xylem masses are apparently endarch in structure; stele 3, for example, shows probable protoxylems in both normal and inverse parts at the extreme inner margins. The other steles of the inner series do not show the first-formed tracheides clearly. The partial steles of the second series, however, clearly show endarch structure (Pl. 11. fig. 2) and at their inner margins the medullary rays seem to widen slightly, although they apparently still consist of one row of cells.

In Section A the horizontally running elements of the limb of the central stele are spirally thickened in the majority of cases; a few have bordered pits. In Section B, where the limb is much larger, most of the elements show a double series of bordered pits (Pl. 11. fig. 5).

* See page 89, reference to enclosure of xylem in periderm.

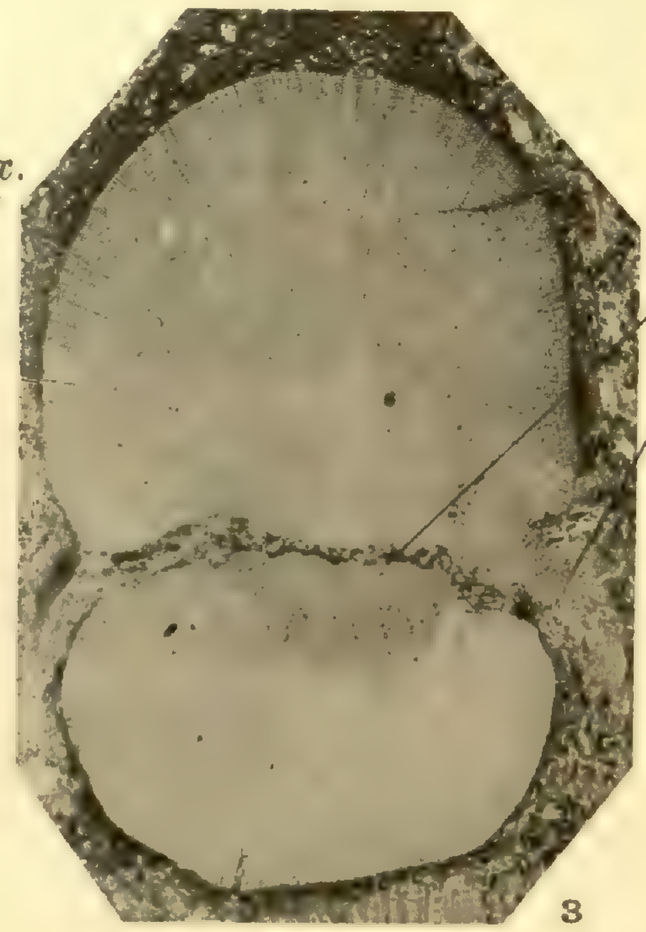
RHEXOXYLON AFRICANUM.

N. B. del.

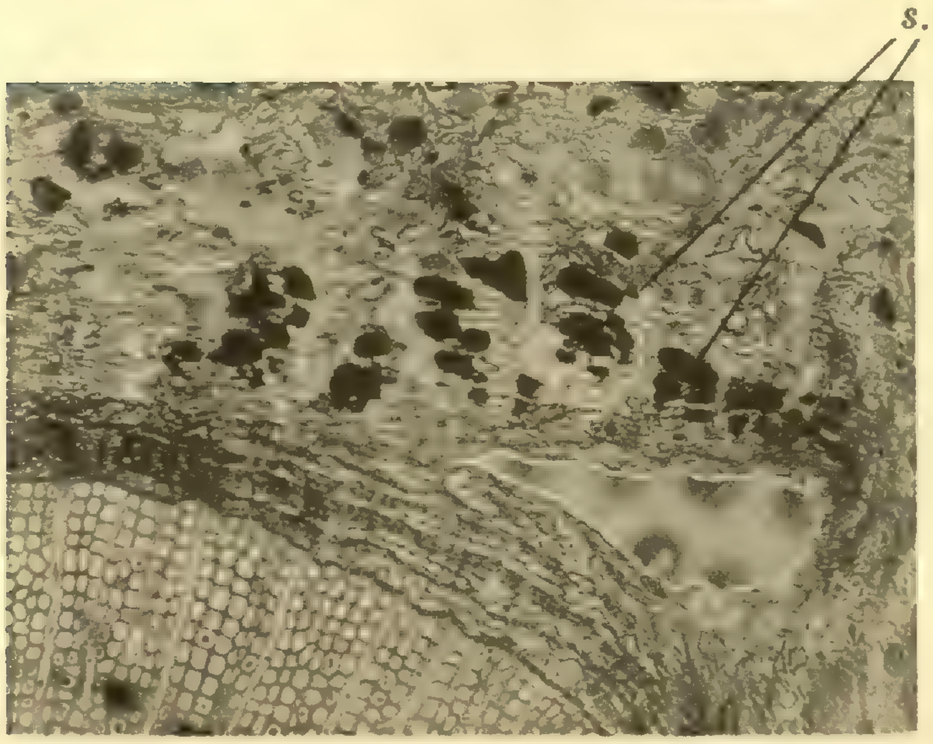
Huth. lith et imp

1

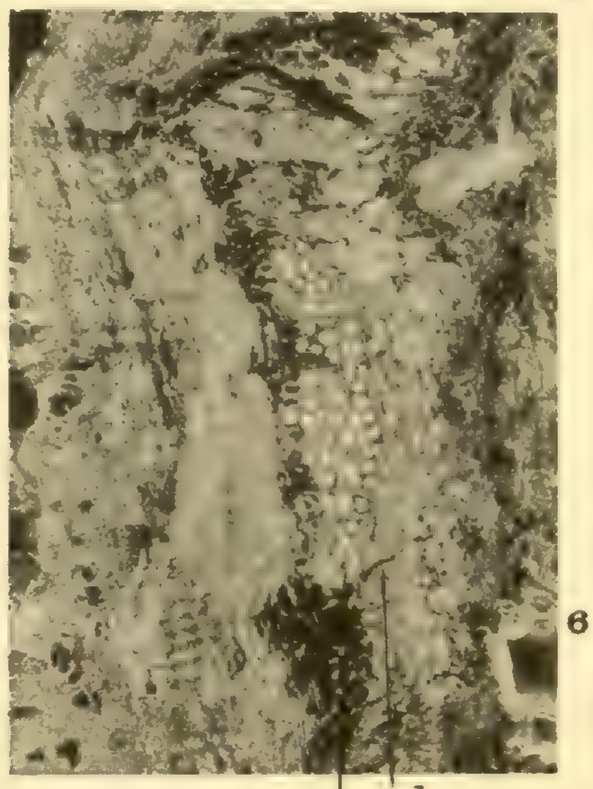
2



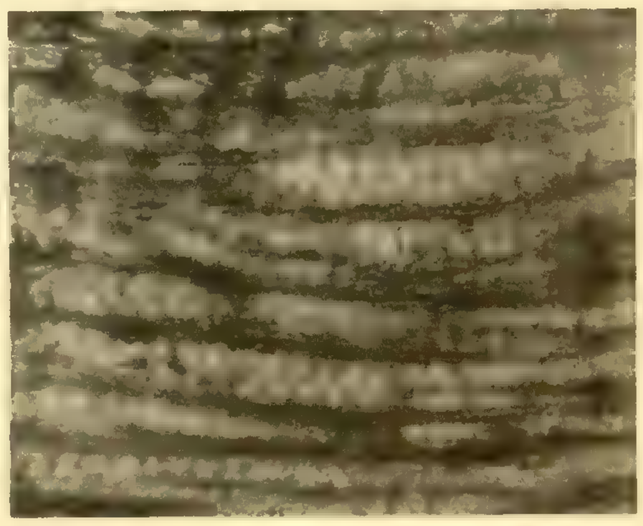
3



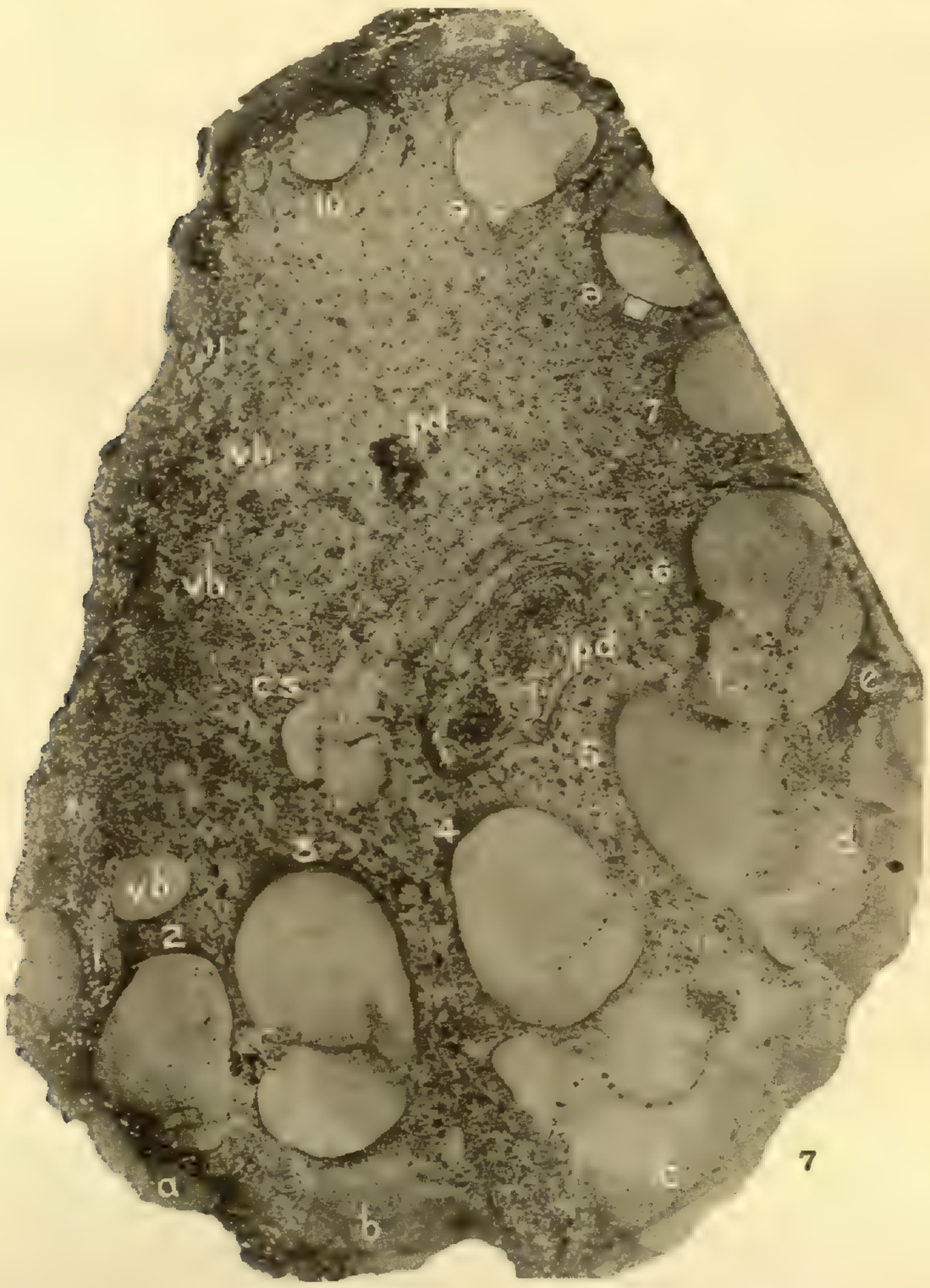
4



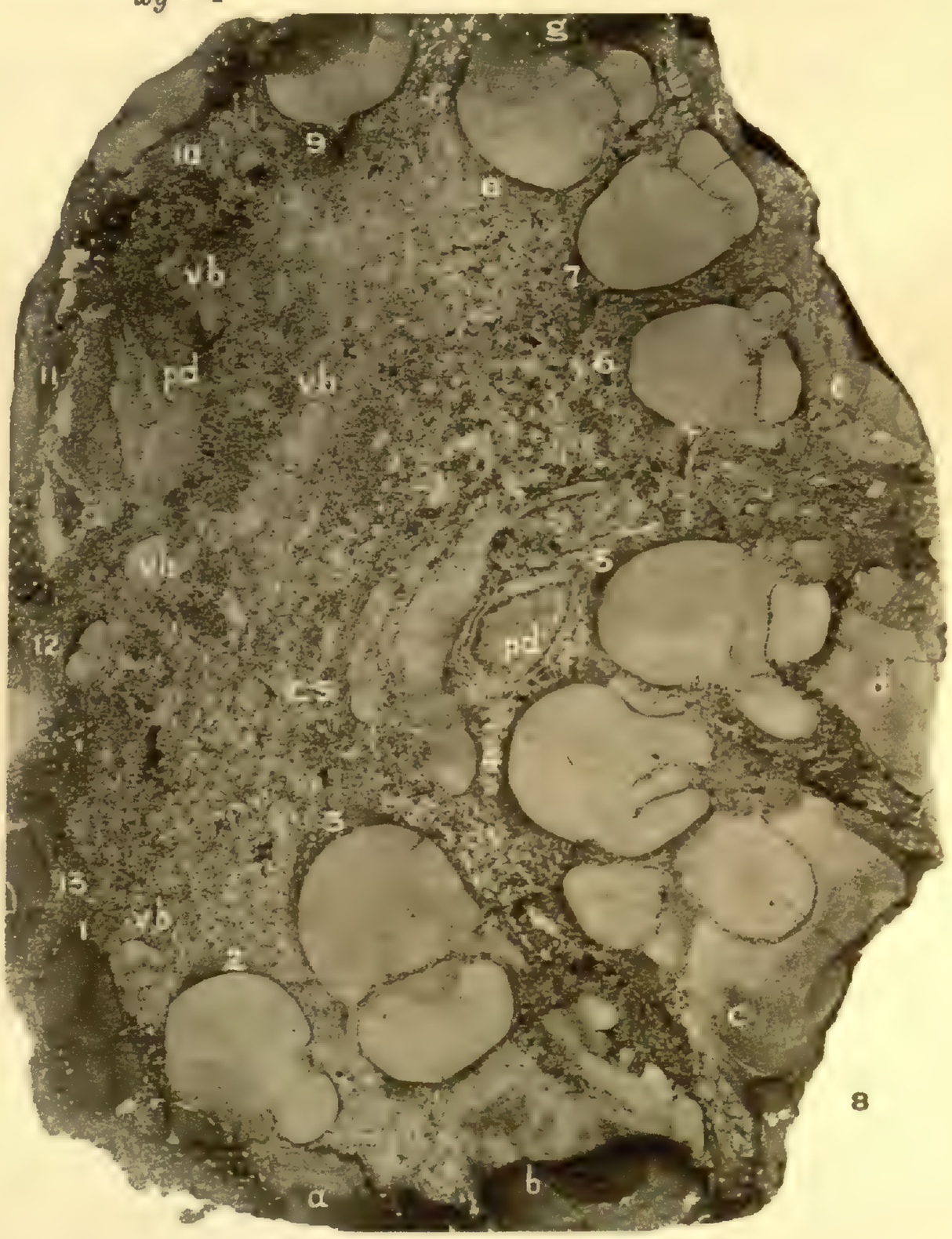
6



5



7



8

W. Tams, Phot.

London Stereoscopic Co. Imp.

RHEXOXYLON AFRICANUM

The lack of structure in the tissue immediately external to the xylem has already been commented upon in dealing with the separate steles. Only here and there are indications of radial rows of thin-walled cells, presumably representing the phloem.

The longitudinal sections add very little to the facts already obtained from the transverse sections. The evidence of the latter with regard to the loose parenchymatous nature of the ground-tissue is confirmed; gum-canals or secretory sacs cannot be distinguished, but patches of sclerotic cells are fairly abundant, especially near the steles. The masses of xylem in longitudinal section show little evidence of branching or anastomosing (*cf.* steles 7 and 8 on cut surface, Pl. 10. fig. 13). In some cases small branches or traces, such as occur in the transverse sections, are seen separating. The brown tissue outlining the xylem is crushed and structureless, as seen in longitudinal sections.

The structure of the xylem may be determined only occasionally in the longitudinal sections. The tracheides have large bordered pits on their radial walls, typically in two alternating series (Pl. 10. fig. 17 *a*; Pl. 11. fig. 5), although here and there only one series, and in one or two cases three series, are present (Pl. 10. fig. 17 *b*). The pits are always in contact and are usually flattened, resembling those of the Cordaiteæ and Araucarieæ. Where the wood is cut tangentially sections of the bordered pits are seen, but the middle lamella is not definitely distinguishable in any of the cases noted. The medullary rays, as seen in tangential section, are fairly high, consisting of three or four to fifteen cells in a vertical series. Their uniseriate nature is clearly shown (Pl. 10. fig. 18).

In the main masses of vascular tissue there are no indications of protoxylem in longitudinal section, but in the ground-mass between two of the steles is a strand of xylem consisting almost entirely of spiral elements.

(c) *Summary of Structure.*

(1) The stem-fragment under consideration shows parts of two series of vascular structures embedded in a parenchymatous ground-mass, which also contains a central arched stele and many isolated patches of vascular elements; sclerotic nests and bands of periderm occur irregularly in the ground-tissue.

(2) Each of the "steles" of the inner series consists of two parts, the outer small and normally orientated, the inner larger and inversely orientated. The two parts are almost in contact, the tissue between being more or less obliterated.

(3) The members of the second series consist of normally orientated xylem only; they are therefore termed "partial steles."

(4) The steles pursue a fairly straight course through the short length of stem, apparently with little branching or anastomosing. Here and there traces are seen separating from the inverse portions of the inner series; while the lateral portions of the partial steles are much broken and irregular.

(5) The xylem is compact and coniferous in type, having the protoxylem elements at the inner margin of the masses.

(6) The xylem elements have bordered pits arranged typically in two alternating series. The pits are flattened and in contact, as in the Cordaiteæ and Araucarian conifers.

(7) The medullary rays, both primary and secondary, are uniseriate.

(8) The tissue accompanying the xylem-masses externally is much crushed, but occasionally shows traces of thin-walled cells, radially arranged. It is considered as representing phloem.

III. Affinities and Reference of the Specimen.

In many respects the stem-fragment shows an approach to certain members of the fossil group Medulloseæ, the structure of which is well known from the researches of Göppert and Stenzel (2), Weber and Sterzel (13), Solms-Laubach (11), Scott (7, 8, 9), and other authors. The forms included under the genus *Medullosa* have been arranged by Weber and Sterzel in form-cycles, each form-cycle being represented by a typical species with varieties which may or may not be quite distinct. The principal form-cycles are those of *M. stellata*, Cotta, *M. porosa*, Cotta, *M. Solmsii*, Schenk, and *M. Leuckarti*, Göpp. & Stenz. Evidently belonging to the same Medullosean family or plexus are forms from different horizons and showing certain differences in structure and histology from *Medullosa* itself. Such genera are *Steloxylon*, *Sutcliffia*, and *Colpoxylon*. The Cladoxyleæ are a distinct group showing certain points of resemblance to the Medulloseæ. The South African stem agrees most closely in general appearance, at least, with *M. Solmsii*. The characters of this form-cycle may be briefly summarised as follows (see 13, p. 73; Taf. iii. figs. 1–5; Taf. viii. fig. 3):—*M. Solmsii* shows typically two series of plate-rings, each ring representing a stele, and appearing to consist of a normally orientated and an inversely orientated mass of secondary tissue, the lateral portions of the ring being often poorly developed (see 13, Taf. iii. fig. 5; Taf. viii. fig. 3). In variety *typica* the normal and inverse parts of the external rings are equally strongly developed; var. *incrassata* has the normal part most strongly developed; and, lastly, in var. *lignosa* there are several zones of secondary wood and bast outside the two zones of plate-rings. In many cases the "partial pith" containing primary tracheides, and typically occupying the central part of a ring, is practically absent (13, Taf. iii. fig. 5; Taf. viii. fig. 3). It may have been originally insignificant in amount, or it may have become crushed during the life of the plant or during fossilisation (13, p. 74). It seems to have entirely escaped preservation in the cases where a distinct space is seen in the interior of the ring. *Medullosa Solmsii*, according to these authors, has the closest xylem-structure known in the genus *Medullosa* (13, p. 114); nothing seems to be actually known of the type of pitting of the tracheides in *M. Solmsii*, though in the genus, as a whole, multiseriate bordered pits are the rule. Phloem is not recognisable; the dark-coloured tissue surrounding the steles is almost structureless. In the interior of the stem *M. Solmsii* shows very small star-rings, and in the cortex also are similar structures arising from the inner series of plate-rings.

The age of *Medullosa Solmsii* and of other Continental species is Permian (13, p. 48); the English species, *M. anglica*, however, is of Lower Coal Measure age (7, p. 84).

In the case of the South African stem, the general appearance and arrangement of the innermost series of steles recalls that of the plate-rings of *M. Solmsii*, except that in the African type the inverse part is much more strongly developed than the normal part, possibly because towards the centre of the stem there is more space for such development to proceed after the second zone of xylem-masses has begun to develop, cramping the normal parts of the first zone. It has been shown, however, that there is variation in the relative degrees of development of the normal and inverse parts of the rings in *M. Solmsii*; while in *M. porosa*, in the case of the outer bundles of the pith (13, p. 70) and sometimes in *M. anglica* (7, p. 89), there is greater development of xylem towards the central parts of the stem. Further, in the South African stem the outer plate-rings are not represented, unless the portions of normally orientated xylem at the periphery of the fragment correspond to these, the inverse parts being absent. Or, these masses may belong to an outer zone of normally orientated tissue, such as occurs in *M. Solmsii*, var. *lignosa*, although in this form the zone is more or less continuous. The outer plate-rings in this case would be entirely unrepresented.

The new stem shows agreement with *M. Solmsii*, and differs from *M. stellata* and *M. porosa*, in the extreme reduction or at least non-preservation of partial pith and primary tracheides. There is a marked difference from *M. anglica*, the steles of which show a large primary mass of tracheides and parenchyma (7, p. 88). The isolated irregularly orientated xylem-groups which occur in the South African stem may be vestigial star-rings, comparable with those very generally present in the central ground-mass of *Medullosa* stems.

The bundles arising from the inner ring of steles in the new type may be of the same nature as the leaf-traces, which in *Medullosa* typically arise from the inner plate-rings. Their ultimate fate, however, cannot be decided, as no cortex is present.

Secretory canals, which are present in the central ground-tissue of *M. Leuckarti* (13, p. 133) and in the ground-tissue and pericycle of the steles in *M. anglica* (7, p. 96), have not been distinguished in the South African stem, nor can they with certainty be shown to occur in species of *Medullosa* other than the two mentioned.

Sclerotic nests are present in the ground-tissue of the African stem; according to Weber and Sterzel, however, their presence in the species of *Medullosa* is uncertain (13, p. 115). Sclerenchymatous bands, isolated in the ground-tissue, are mentioned by Scott for *M. anglica* (7, p. 96; pl. x. fig. 2); while for the same species internal periderm is described (7, p. 96; pl. v. figs. 1 & 3; pl. vii. fig. 13; pl. x. figs. 6 & 7), occurring in a continuous though irregular zone. In the African stem isolated bands of periderm occur apparently without definite purpose.

Owing to the variability and wide range of structure shown by *Medullosa* stems, the only distinct points of difference between them and the South African stem lie in the compact wood of the latter, with its uniseriate medullary rays, and in the pitting of the tracheides. In the new specimen the biseriate pitting of the tracheides resembles that exhibited by the Cordaiteæ and Araucarieæ rather than the multiseriate type

occurring in the species of *Medullosa* and in Pteridosperms generally. It is unfortunate that, as mentioned above, nothing is known of the pitting in *M. Solmsii*, which shows an approach to the South African stem in the more compact nature of the xylem and also in the apparent reduction of "partial pith."

Steloxylon Ludwigii, a stem of doubtful Permian age, is another member of the Medullosean group. It was first somewhat superficially described by Göppert and Stenzel as *Medullosa Ludwigii* (2, Taf. xvii. figs. 18–20; see also 6, Taf. i. figs. 1–16; and 12, Taf. iii. figs. 6 & 9); it exhibits a homogeneous ground-tissue with usually roundish or elliptical steles. Some are, however, considerably elongated and arranged somewhat radially, instead of tangentially as in the case of the plate-rings of *Medullosa*. The structure of the ground-tissue is not clear, but appears to have been parenchymatous. The medullary rays of the wood are of varying heights, and are uni- or biseriate, separating groups of two or three series of tracheides. The tracheides bear roundish oval bordered pits in one or more rows. Phloem is not preserved; while the steles have a partial pith, the structure of which is not clear. *Steloxylon Ludwigii* differs from the species of *Medullosa* and from the South African stem in the arrangement of the steles. It approaches the new type in the pitting of the tracheides, but differs from it in the less constantly uniseriate nature of the medullary rays and in the definite presence of a partial pith (12, p. 552).

Sutcliffia insignis, from the Lower Coal Measures of Shore, is considered by Scott (8) to be a probable primitive type of Medullosean stem. The recent work of Dr. E. de Fraine indicates its affinities with *M. anglica*. It possesses a large central stele, very similar in structure to a single stele of *M. anglica*. From the main stele arise subsidiary steles at intervals. Phloem is well preserved, and the tracheides usually possess multiseriate bordered pits. *Sutcliffia* is not comparable with the South African stem, except through other members of the Medullosean group.

Colpoxylon, represented by the species *C. æduense*, Brongn., has been described by Renault as coming from the Permian of Autun (4, pl. 67, figs. 1 & 2). It is in agreement with regard to structure with some of the simpler Medulloseæ, but it is monostelic for some length of the stem. It is perhaps an aberrant *Medullosa*, and like *Sutcliffia* is only indirectly comparable with the South African stem.

The Cladoxyleæ are a group of forms (*Cladoxylon* and *Völkelia*) approaching the Medulloseæ in the possession of numerous steles. Solms described the structure of *Cladoxylon* in 1896 (10) and of *Völkelia* in 1910 (12). The group differs from the Medulloseæ in the arrangement of the steles, which are usually more or less radially disposed (cf. *Steloxylon*), and also in the minute structure of the wood, the tracheides usually having scalariform pits. The age of the group is Devonian or at least early Palæozoic. Scott concludes that the Cladoxyleæ and Medulloseæ have no intimate relation, but they probably present a case of parallel development, showing superficial resemblances to each other in the possession of many steles (8, p. 64; 9, p. 497).

Cladoxylon Kidstoni, however, deserves mention on account of an approach in certain characters to the South African fossil. It has been described by Solms-Laubach as coming from the Lower Carboniferous of Berwickshire (12, p. 537). As the stem-

fragment is very small (2·4 cm. ×2 cm. diam. and 1·3 cm. long), only four steles and part of two others being represented, it is impossible to determine the original arrangement of vascular structures. If anything may be judged from the position of those present, however, it would seem that they were more or less radially arranged—that is, the narrow partial pith lay in a radial direction. The steles are almost complete rings; only at one pole of the partial pith is the continuity of the secondary growth broken, and at this point, in the case of two of the steles, is attached a peculiar wing-like mass of secondary elements, probably representing a trace. In one instance, the wing is less closely in contact with the main stele and has divided into two parts (12, Taf. iii. fig. 5). At the other pole of the stele, secondary growth shows its greatest development. The partial pith is narrow and, like the phloem, usually not preserved: in one case its cellular nature may be determined (12, Taf. iii. fig. 11). The steles pursue a fairly straight course, so far as can be determined from the fragment. The wood is compact, with uniseriate rays separating groups of from two or three to eight or nine rows of tracheides (12, Taf. iii. fig. 11). In this there is agreement with the South African fossil. The chief feature of interest in *C. Kidstoni*, from the point of view of comparison of the two types, lies in the pitting of the tracheides. The radial walls possess typically a single series of elongate-elliptical bordered pits, giving a scalariform effect (*cf.* character of the group Cladoxyleæ). Here and there, however, often in the same tracheide with the single series, a double row of bordered pits occurs (12, Taf. iii. fig. 7) *, the pits being either alternate or opposite—they are always flattened and in contact. In the case of alternate pitting the appearance is very similar to that presented by the tracheides of the South African fossil. This cannot, however, be regarded as indicating any relationship between the two types, which show points of dissimilarity in other respects, such as stelar organisation. *C. Kidstoni* is interesting, in that the pitting of its tracheides points to a transition from a simpler more fern-like type to that exhibited by the South African fossil, Cordaiteæ, and Araucarieæ. The Cladoxyleæ need not be considered so far as the closer relationships of the new type are concerned, but must be mentioned with the Medulloseæ as representative of the plexus of polystelic types to which the stem under consideration is apparently referable.

With regard to the wider affinities of the new specimen, it is possible that the biseriate Araucarian type of pitting exhibited by its xylem elements indicates a point of contact more or less remote with the ancestral forms of the Araucarieæ. The combination of Araucarian pitting of the xylem elements with the Medullosean arrangement of steles is interesting, and the possibility is suggested that there may have existed other simpler or even monostelic forms, as yet unknown, also exhibiting Araucarian pitting, and that from these or their ancestral stock the Araucarieæ may have been derived either directly or indirectly. It is extremely unsafe to base any conclusions upon the pitting of the xylem elements, for how far such a character may serve as a criterion in the consideration of relationship between types is not as yet thoroughly understood, and the above suggestion is made with due regard to this fact. It is, however, interesting

* In Solms-Laubach's figures the bordering of the pits is not shown.

in that it provides a parallel case to that put forward by Miss de Fraine (1) for the Cycadaceæ, which she considers may have originated from a monostelic Medullosean form typified by *Sutcliffia* *, which shows a more Cycadean type of pitting.

The age of the South African specimen, as has been shown, is doubtful, but its structure justifies its reference to the Palæozoic era, while its agreement in general anatomy with the Continental Medulloseæ rather than with the earlier English types is consistent with reference to an Upper Permian horizon.

From early Palæozoic to Permian times there seems to have been a plexus of types showing polystelic structure, and the South African stem may be included as a member of this plexus. To recapitulate its probable affinities:—The stem seems to agree most closely with the genus *Medullosa*, which is recognised as showing considerable variation of stelar structure. It differs from the typical species †, however, in the extreme reduction of the partial pith, in the general coniferous texture of the xylem with its compact structure and uniseriate rays, as well as in the pitting of the elements, which in this respect resemble those of the Cordaiteæ or the Araucarian conifers. *Steloxylon* is approached chiefly in the type of pitting of the tracheides, but it differs in the less definite arrangement of the steles and in the presence of a partial pith—this being much reduced in the South African stem.

These differences, united to the facts that the horizon and locality of the stem-fragment are indefinite and that its associations are indeterminable, sufficiently isolate it from all hitherto-described types to render its reference to any one of them undesirable. Further, this fossil appears to be the first, and so far the only, specimen of a stem of this nature known from the Southern Hemisphere, so that it seems justifiable to institute a provisional genus for its reception and to include the genus in the family Medulloseæ.

The generic name *Rhexoxylon* ‡ is suggested as being descriptive of the broken-up nature of the vascular structures of the stem.

IV. Summary and Diagnosis.

(1) *Rhexoxylon africanum*, a stem-fragment of doubtful later Palæozoic age, from an unknown South African locality, is described and diagnosed as follows:—

Rhexoxylon, nov. gen.

Vascular system of the stem consisting of an inner ring of elliptical steles, each composed of a large inversely orientated part, from which traces are given off, and a small normal part; external to these a series of "partial steles" consisting only of normally orientated elements; the lateral margins of these partial steles often much broken by the separation of traces. Xylem compact, having spiral elements on the inner margin;

* *Cf.* Worsdell's views on the origin of Cycadean structures.

† *M. Solmsii* must be excepted. Note remarks on p. 96.

‡ Gr., *ῥηγνυμι*—I break up.

metaxylem elements typically with biseriate bordered pits. Medullary rays uniseriate. Ground-tissue parenchymatous, with scattered and irregular vascular strands, bands of periderm, and sclerotic nests.

R. AFRICANUM, nov. sp.
Characters of the genus.

(2) The general structure of *Rhexoxylon africanum* suggests relationship with the genera *Medullosa* and *Steloxylon*, and the new genus is included in the family Medulloseæ.

In conclusion, the writer's expressions of gratitude are due to Professor Seward for help and advice during the above investigation; and also to Dr. R. Kidston for slides of *Cladoxylon Kidstoni* which he kindly lent for comparison with the South African stem.

Botany School, Cambridge.

REFERENCES.

(1) DE FRAINE, E.—On the Structure and Affinities of *Sutcliffia*, in the light of a newly discovered Specimen. Ann. of Bot. vol. xxvi. 1912.
(2) GÖPPERT, H. R., and STENZEL, G.—Die Medulloseæ, eine neue Gruppe der fossilen Cycadeen. Palæontographica, 1881.
(3) HOLDEN, H. S.—Note on a wounded *Myeloxylon*. New Phyt. vol. ix. 1910.
(4) RENAULT, B.—Bassin Houiller et Permien d'Autun et d'Epinac. Flore Fossile, iv. pt. II. 1896.
(5) ROGERS, A. W., and DU TOIT, A. L.—An Introduction to the Geology of Cape Colony. 1909.
(6) SCHENK, A.—Ueber *Medullosa*, Cotta, und *Tubicaulis*, Cotta. Abhandl. der math. phys. Cl. der k. Sächs. Gesellschaft der Wissenschaften, vol. xv. no. vi. 1889.
(7) SCOTT, D. H.—Structure and Affinities of Fossil Plants from the Palæozoic Rocks. III. On *Medullosa anglica*, a new Representative of the Cycadofilices. Phil. Trans. Roy. Soc. B, vol. cxci. 1899.
(8) —— On *Sutcliffia insignis*, a new Type of Medulloseæ from the Lower Coal Measures. Trans. Linn. Soc. vol. vii. p. 45. 1906.
(9) —— Studies in Fossil Botany. 1909.
(10) SOLMS-LAUBACH, H. GRAF ZU.—Ueber die Seinerzeit von Unger beschriebenen structurbietenden Pflanzenreste des Unterculm von Saalfeld in Thüringen. Abhandl. der k. pr. geologischen Landesanstalt, Neue Folge, Heft 23. 1896.
(11) —— Ueber *Medullosa Leuckarti*. Bot. Zeit. vol. lv. p. 175. 1897.
(12) —— Ueber die in den Kalksteinen des Culm von Glätzisch-Falkenberg in Schlesien erhaltenen structurbietenden Pflanzenreste. IV.—*Völkelia refracta, Steloxylon Ludwigii*. Zeitschrift für Botanik, 1910.
(13) WEBER, O., and STERZEL, J. T.—Beiträge zur Kenntniss der Medulloseæ. Ber. der Naturw. Ges. zu Chemnitz, vol. xiii. 1896.
(14) WORSDELL, W. C.—The Structure and Origin of the Cycadaceæ. Annals of Botany, vol. xx. p. 129. 1906.

EXPLANATION OF THE PLATES.

Plate 10.

Figures 1–12 diagrammatic, figures 14–18 drawn with the aid of a camera lucida.

Fig. 1. Transverse surface of the stem, after cutting, showing the main features (*cf.* Pl. **11.** fig. 8, a photograph of the complete Section A, taken from this surface, and representing a level slightly higher in the stem) : 1–13, steles of the inner series ; *a–g*, partial steles of the outer series. Nat. size.

Figs. 2–8. Transverse sections of the vascular structures of the stem, drawn from the complete Section A, shown in Pl. **11.** fig. 8. Comparison should be made with this and with fig. 1 for the relative positions of the vascular masses of the stem. *tr* signifies transverse section of the xylem elements ; *ob*, oblique section ; and *lg*, longitudinal section. The shaded outlining of the steles indicates the brown crushed tissue.

Fig. 2, stele 3 of the inner series : *pm*, partial pith ; *px*, protoxylem ; at *ob* a trace is seen separating from the larger inverse part of the stele. Fig. 3, steles 4 and 5 of the inner series, and partial steles *c* and *d* of the outer series : α and β, normal and inverse xylem, respectively, of the inner steles ; γ, xylem evidently belonging to β, but more or less separated from it by breaks in the continuity of the radial series of elements : similar breaks are seen in partial stele *c* ; *s*, sclerotic nests. Figs. 4, 5, and 6, steles 6, 7, and 8, respectively. Fig. 7, stele 9, showing sclerotic nests in the crushed tissue at *s*. Fig. 8, central stele ; *pd*, bands of periderm. Figs. 2–7, ×3 ; fig. 8, ×5.

Fig. 9. Central stele, at a slightly higher level than fig. 8. (From an incomplete Section.) ×5.

Figs. 10 & 11. Vascular structures at the level of Section B, shown in Pl. **11.** fig. 7. Fig. 10, steles 5 and 6 of the inner series, and partial steles *d* and *e* of the outer series : *vb*, isolated and irregular vascular strands ; other lettering as before. ×3. (*Cf.* figs. 3 & 4.) Fig. 11, central stele : xy^a, xylem elements enclosed in periderm ; xy^b, xylem elements scattered in ground-mass. ×5. (*Cf.* figs. 8 & 9.) For the position of the central stele as shown in figs. 8, 9, & 11, relative to that of the other vascular structures of the stem, refer to fig. 1 and Pl. **11.** figs. 7 & 8.

Fig. 12. Diagram showing the relation between the vertically striated bands of the outer surface of the stem (*cf.* Pl. **11.** fig. 1) and the vascular masses of the cut transverse surface. Nat. size.

Fig. 13. Portion of a tangential longitudinal surface, showing the straight course of two inner steles (7 and 8) : *a*, ground-mass. Nat. size.

Fig. 14. Xylem elements, showing the layered siliceous filling of the cell-cavities (see also figs. 15 & 18). Note indication of middle lamella, *ml*. ×450.

Fig. 15. Protoxylem group of stele 3 (*cf.* fig. 2). ×450.

Fig. 16. Sclerotic nests in the crushed tissue of stele 9. ×90. (*Cf.* fig. 7, *s*, and Pl. **11**, fig. 4.)

Fig. 17. Pitting of the tracheides : *a*, typical ; *b*, from the limb of the central stele. ×280. (*Cf.* Pl. **11.** fig. 5.)

Fig. 18. Tangential section of xylem, showing the uniseriate medullary rays. Note the layering of siliceous material in the cells of the rays. ×280.

Plate 11.

Fig. 1. A photograph of the decorticated stem-fragment, showing the external appearance: *a*, ground-tissue; *st*, stelar tissues. Nat. size.

Fig. 2. The inner margin of partial stele *b*, showing protoxylems (*px*) and uniseriate medullary rays (*mr*). ×70.

Fig. 3. Stele 3, from Section A (*cf.* fig. 8), a fairly typical example of an inner stele: *t*, trace; *pm*, partial pith. ×5. Note the arrangement of the xylem elements and the outlining of dark crushed tissue.

Fig. 4. Brown tissue of stele 10 (from Section B), showing radial arrangement of elements: *s*, sclerotic nests. ×70. Note the structure of the xylem, with uniseriate medullary rays.

Fig. 5. Xylem elements, showing biseriate pitting. ×325.

Fig. 6. Portion of periderm band in arch of central stele (Section B). The periderm (*pd*) encloses a strand of xylem elements (xy^a). ×70. (*Cf.* Pl. **10**. fig. 11.)

Figs. 7 & 8. Sections B and A respectively. ×2. Steles and partial steles are numbered and lettered as in Pl. **10**. fig 1: *cs*, central stele; *pd*, epiderm bands; *vb*, isolated vascular strands.

LINNEAN SOCIETY OF LONDON.

MEMORANDA CONCERNING TRANSACTIONS.

The First Series of the Transactions, containing both Botanical and Zoological contributions, has been completed in 30 Vols., and a few entire sets are still for sale. Only certain single volumes, or parts to complete sets, may be obtained at the original prices. The price of the Index to Vols. 1–25 is 8*s.* to the public, and 6*s.* to Fellows: to Vols. 26–30, 4*s.* to the public, and 3*s.* to Fellows.

The Second Series of the Transactions is divided into Zoological and Botanical sections. The prices of the Botanical parts of these which have been published are as undermentioned. (For the Zoological parts see Zoological wrapper.)

SECOND SERIES.—BOTANY.

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
I.	Parts I.–IX. (complete).						
	1875–80.	8	1	0	6	1	0
II.	Parts I.–XVI. (complete).						
	1881–88.	6	16	10	5	2	3
III.	Part I. 1888.	3	12	0	2	14	0
	Part II. 1891.	0	5	0	0	3	9
	Part III. 1891.	0	7	0	0	5	3
	Part IV. 1891.	0	6	0	0	4	6
	Part V. 1891.	0	6	0	0	4	6
	Part VI. 1891.	0	3	6	0	2	8
	Part VII. 1892.	0	6	0	0	4	6
	Part VIII. 1893.	0	6	0	0	4	6
	Part IX. 1893.	1	8	0	1	1	0
	Part X. 1894.	0	10	0	0	7	6
	Part XI. 1894.	0	3	4	0	2	6
IV.	Part I. 1894.	1	0	0	0	15	0
	Part II. 1894.	2	0	0	1	10	0
	Part III. 1895.	2	10	0	1	17	0
	Part IV. 1895.	0	3	4	0	2	6
V.	Part I. 1895.	0	9	0	0	6	9
	Part II. 1895.	0	12	0	0	9	0
	Part III. 1896.	0	6	0	0	4	6
	Part IV. 1896.	1	0	0	0	15	0
	Part V. 1896.	0	14	0	0	10	6
	Part VI. 1896.	0	4	0	0	3	0
	Part VII. 1897.	0	4	0	0	3	0
	Part VIII. 1897.	0	6	0	0	4	6
	Part IX. 1899.	0	12	0	0	9	0
	Part X. 1899.	0	6	0	0	4	6
	Part XI. 1899.	0	7	0	0	5	3
	Part XII. 1899.	0	12	0	0	9	0
	Part XIII. 1900.	0	1	6	0	1	2
	Part XIV. 1900.	0	3	0	0	2	3
	Part XV. 1901.	0	6	0	0	4	6

SECOND SERIES.—BOTANY (*continued*).

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
VI.	Part I. 1901.	1	10	0	1	2	6
	Part II. 1901.	0	6	0	0	4	6
	Part III. 1902.	0	18	0	0	13	6
	Part IV. 1903.	0	8	0	0	6	0
	Part V. 1903.	0	8	0	0	6	0
	Part VI. 1903.	0	12	0	0	9	0
	Part VII. 1904.	0	12	0	0	9	0
	Part VIII. 1904.	0	12	0	0	9	0
	Part IX. 1904.	0	7	0	0	5	3
	Part X. 1904.	0	14	0	0	10	6
	Part XI. 1905.	0	4	0	0	3	0
VII.	Part I. 1904.	0	5	0	0	3	9
	Part II. 1905.	0	6	0	0	4	6
	Part III. 1906.	0	3	0	0	2	3
	Part IV. 1906.	0	7	0	0	5	3
	Part V. 1907.	0	10	0	0	7	6
	Part VI. 1907.	0	4	0	0	3	0
	Part VII. 1907.	0	6	0	0	4	6
	Part VIII. 1908.	0	5	0	0	3	9
	Part IX. 1908.	0	2	6	0	2	0
	Part X. 1908.	0	7	0	0	5	3
	Part XI. 1909.	0	4	0	0	3	0
	Part XII. 1909.	0	12	0	0	9	0
	Part XIII. 1909.	0	5	0	0	3	9
	Part XIV. 1909.	0	6	0	0	4	6
	Part XV. 1910.	0	6	0	0	4	6
	Part XVI. 1912.	0	3	0	0	2	3
	Part XVII. 1912.	0	8	0	0	6	0
	Part XVIII. 1912.	0	5	0	0	3	9
	Part XIX. 1912.	0	3	0	0	2	3
	Part XX. Index.	0	3	0	0	2	3
VIII.	Part I. 1913.	1	0	0	0	15	0
	Part II. 1913.	0	8	0	0	6	0

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

MARINE ALGÆ, RHODOPHYCEÆ, OF THE 'SEALARK' EXPEDITION, COLLECTED BY MR. J. STANLEY GARDINER, M.A.

BY

MRS. A. WEBER-VAN BOSSE, PH.D.

(*Communicated by* Prof. J. STANLEY GARDINER, M.A., F.R.S., F.L.S.)

LONDON:

PRINTED FOR THE LINNEAN SOCIETY

BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON-HOUSE, PICCADILLY, W.,

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

October 1913.

IV. *Marine Algæ*, Rhodophyceæ, *of the 'Sealark' Expedition, collected by Mr. J. Stanley Gardiner, M.A.*

By Mrs. A. Weber-van Bosse, *Ph.D.* (*Communicated by* Professor J. Stanley Gardiner, *M.A., F.R.S., F.L.S.*)

(Plates 12–14 and 1 text-figure.)

Read 5th June, 1913.

I. Introduction.

The algæ treated of in the following paper were collected by Mr. J. Stanley Gardiner during the Percy Sladen Trust Expedition to the Indian Ocean in 1905. It was at first intended that Mrs. A. Gepp should work out the collection, but she handed it over to me, and illness prevented her joining in the work, which we would only have been too glad to carry out together. She had, however, sorted the material before sending it to me.

The collection does not contain all the Rhodophyceæ collected by Mr. Stanley Gardiner; the *Lithothamnia* have been worked out by the late lamented Mr. Foslie. The literature on the algæ of this part of the Indian Ocean is scarce, for besides the paper by Mr. Foslie and the Report on the Chlorophyceæ and Phæophyceæ of the 'Sealark' Expedition by A. Gepp, M.A., F.L.S., and Mrs. E. Gepp, I only know of one paper in which more than a few algæ of this region are mentioned. Mr. Reinbold, in "Meeresalgen der Deutschen Tiefsee-Expedition," mentions 26 species of Rhodophyceæ from Diego Garcia and Mahé, 10 of which have been also collected by Mr. Stanley Gardiner. Besides this paper of Mr. Reinbold, I have found two other short references to algæ from Diego Garcia and the Seychelles. Mr. W. B. Hemsley adds a note on Algæ to his "Report on the Vegetation of Diego Garcia." Of the algæ named only *Dasya indica*, J. Ag., has any interest for us at present; it is the only Red alga mentioned. A note by "J. B." in 'Knowledge' treats only of Myxophyceæ, and may therefore be passed over in silence.

The 'Sealark' collection had special interest for me because I am just publishing, with the aid of Mr. Reinbold, the first part of a list of algæ collected during the 'Siboga' Expedition in the Malay Archipelago. This part contains the Myxophyceæ, Chlorophyceæ, and the Phæophyceæ; the second part, containing the Rhodophyceæ, will, I hope, follow soon. The study of a region so near to the Malay Archipelago afforded me great interest from a phyto-geographical standpoint. It had, however, one drawback; some species found by me in the 'Siboga' collection and recognized as new are also found in the Stanley Gardiner collection, and the fact that the paper on the algæ of the Indian Ocean will appear before the Siboga paper, will diminish the number of novelties in the latter. But this could not be avoided, and I have described the new species as fully as I could; only in one case, when the barren, small fragment could not possibly have been recognized apart from the fertile specimens of the 'Siboga' Expedition, have I referred to the forthcoming paper.

Amongst the algæ of the Indian Ocean I found species of two new genera, *Tapeinodasya* and *Oligocladus*, described for the first time from the Malay Archipelago in 'Les Annales du Jardin botanique de Buitenzorg,' vol. ix. 1910. It afforded me great pleasure to describe these species, which confirm the validity of my new genera. One genus, *Pseudendosiphonia*, is new in the present collection; it is most closely allied to *Endosiphonia*, and yet is so different that it can be easily distinguished; one species, *Dasya indica*, had to be described as a new genus—*Amphisbetema*.

Many of the algæ are barren, and can therefore not be specifically named; others are only fragments. I have given the generic names of all, because I think that, for our knowledge of the geographical distribution, even a generic name may have some value. The collection is rich in novelties; I often hesitated before describing a given alga as new, but when, after careful investigation, I could not identify it with any existing diagnosis, I felt I had no alternative. Of the novelties, which include one genus, 17 species, one variety and one form, 11 are from deep water, 2 from reef and deep water, 7 from reef alone. It may be well to recall here that Mr. and Mrs. Gepp found *Avrainvillea amadelpha* in material from reef and deep water. Many algæ appear to accommodate themselves to both modes of living. The 'Sealark' Expedition had, like the 'Siboga' Expedition, the advantage of the use of a dredge, and several hauls from deep water, where many Rhodophyceæ flourish, have given a rich harvest. The nature of the bottom surrounding the reefs and islands, whence these algæ come, has been treated in detail in the above-mentioned paper by Mr. Foslie. I think it therefore unnecessary to do this again.

The geographical distribution shows that a great resemblance exists between the algological flora of the Indian Ocean and that of the Malay Archipelago as well as that of the east coast of Africa. Of the 26 species found at Mahé and Diego Garcia by the "Deutsche Tiefsee-Expedition," 7 occur also at Dar-es-Salaam, and of the 8 other species collected at Dar-es-Salaam by that expedition 5 are found in the Stanley Gardiner collection *. But it is a puzzle to know how *Cladhymenia oblongifolia* and *Calliblepharis prolifera*, only known hitherto from New Zealand, and *Chondria pusilla*, only known from the West Indies, came to be inhabitants of the present region. It emphasizes the fact that the geographical distribution of algæ is a factor that should always be very carefully considered. The finding of *Peyssonnelia Harveyana*, known only from the Atlantic Ocean at Brest, puzzled me less, because it may be possible that the determination of the barren plant is erroneous. I have therefore queried it.

I have given a list of the localities with the algæ found at each, and a general list of all the Rhodophyceæ collected by Mr. Stanley Gardiner. The systematic observations on the different genera and species conclude the paper.

I wish here to express my sincere thanks to Mr. Stanley Gardiner for entrusting me with his collection, and to Messrs. Gepp and Cotton for the kind help they have given me; and I may perhaps add a word of deep-felt regret that Mrs. Gepp was unable to do her share of the work.

* The number of species common to both regions is probably far greater, for in the recently published paper by Br. Schröder, "Zellpflanzen von Ost-Afrika," Hedwigia, Bd. lii., four more species are mentioned, also found in the present collection.

II. List of Localities and Names of the Algæ found at each of them.

Chagos Archipelago: Diego Garcia, Egmont, Salomon, Peros (Île du Coin).

1. *Gelidium crinale* (Turn.), Lamx.; 2. *Gelidiopsis rigida* (Vahl), Web. v. B.; 3. *Hypnea pannosa*, J. Ag.; 4. *Laurencia obtusa* (Huds.), Lamx.; 5. *L. spinulifera*, Kütz.; 6. *L. pygmæa*, n. sp.; 7. *Chondria pumila*, Vick.; 8. *Herposiphonia prorepens* (Harv.), Schm.; 9. *Dasyopsis Geppii*, n. sp.; 10. *D. palmatifida*, n. sp.; 11. *Dictyurus purpurascens*, Bory; 12. *Antithamnion adnatum*, J. Ag.; 13. *Ceramium cinnabarinum* (Gratel.), Hauck; 14. *Reinboldiella Schmitziana* (Reinb.), de Toni; 15. *Peyssonnelia calcea*, Heydr.; 16. *Melobesia callithamnioides*, Falk.; 17. *Amphiroa fragilissima* (Linn.), Lamx.; 18. *Jania tenella*, Kütz.

Coetivy, reef.

1. *Chantransia Liagoræ*, n. sp.; 2. *Liagora orientalis*, J. Ag.; 3. *L. hawaiiana*, Butt.; 4. *Gelidium pannosum*, Grun.; 5. *Champia compressa*, Harv.; 6. *Laurencia obtusa* (Huds.), Lamx.; 7. *L. papillosa* (Forsk.), Grev., f. *australica* in herb. Kütz.; 8. *L. ceylanica*, J. Ag.; 9. *Oligocladus Prainii*, n. sp.; 10. *O. pusillus*, n. sp.; 11. *Dasyopsis aperta*, n. sp.; 12. *D. Geppii*, n. sp.; 13. *D. palmatifida*, n. sp.; 14. *Heterosiphonia* spec., fragment; 15. *Dictyurus purpurascens*, Bory; 16. *Jania tenella*, Kütz.

Seychelles Archipelago (various localities).

1. *Sarconema furcellatum*, Zan.; 2. *Gelidiopsis variabilis* (Grev.), Schm.; 3. *Corallopsis Cacalia*, J. Ag.; 4. *Hypnea Valentiæ*, Turn.; 5. *H. pannosa*, J. Ag.; 6. *Champia* spec.; 7. *Laurencia papillosa* (Forsk.), Grev., f. *australica* in herb. Kütz.; 8. *Acanthophora orientalis*, J. Ag.; 9. *Roschera* (*Tolypiocladia*) *glomerulata* (Ag.), n. comb., fragment; 10. *Peyssonnelia coccinea*, J. Ag.; 11. *P. biradiata*, n. sp.; 12. *Jania tenella*, Kütz.

Mahé, Cap Ternè, reef.

1. *Dermonema dichotomum*, Harv.; 2. *Galaxaura fastigiata*, Decne.; 3. *Gelidiopsis rigida* (Vahl), Web. v. B.; 4. *Corallopsis Cacalia*, J. Ag.; 5. *Hypnea pannosa*, J. Ag.; 6. *Acanthophora orientalis*, J. Ag.; 7. *Amphiroa fragilissima* (Linn.), Lamx.; 8. *Jania tenella*, Kütz.

Praslin, reef.

1. *Galaxaura Liebmanni* (Aresch.), Kjellm.; 2. *Gelidiopsis rigida* (Vahl), Web. v. B.; 3. *Hypnea pannosa*, J. Ag.; 4. *Polysiphonia* spec., fragment; 5. *Amphiroa foliacea*, Lamx.; 6. *Jania tenella*, Kütz.

Amirante.

1. *Galaxaura veprecula*, Kjellm.; 2. *Iridæa* spec.; 3. *Polycœlia van Hoevellii*, n. sp., fragment; 4. *Gracilaria compressa* (Ag.), Grev.; 5. *Calliblepharis prolifera* (Harv.), J. Ag.; 6. *Hypnea* spec.; 7. *Champia compressa*, Harv.; 8. *Cœlarthrum Albertisii* (Picc.), Börg.; 9. *Hypoglossum* spec. (*spathulatum*, Kütz.?); 10. *Nitophyllum* spec.,

fragment; 11. *Laurencia ceylanica*, J. Ag.; 12. *Pseudendosiphonia Gardineri*, n. g., n. sp.; 13. *Cladhymenia oblongifolia*, Hook. et Harv.; 14. *Dasyopsis Geppii*, n. sp.; 15. *D. palmatifida*, n. sp.; 16. *Tapeinodasya Ethelæ*, n. sp.; 17. *Dictyurus purpurascens*, Bory; 18. *Griffithsia* spec., fragment; 19. *Cryptonemia seminervis*, J. Ag.; 20. *Peyssonnelia polymorpha* (Zan.), Schm., var. *Gardineri*, n. var.

Aldabra (collected by J. C. F. Fryer).

1. *Galaxaura hawaiiana*, Butt.; 2. *Hypnea divaricata* (?), Grev.; 3. *H. pannosa*, J. Ag.; 4. *Laurencia nidifica*, J. Ag.; 5. *L. obtusa* (Huds.), Lamx.; 6. *L. papillosa*, (Forsk.), Grev., f. *australica* in herb. Kütz.; 7. *Chondria simpliciuscula*, n. sp.; 8. *Amphisbetema indica* (J. Ag.), n. n.; 9. *Spyridia filamentosa* (Wulf.), Harv., fragment; 10. *Halymenia polyclada*, A. & E. S. Gepp, var. *aldabradensis*, n. var.

Saya de Malha.

1. *Galaxaura fastigiata*, Decne., fragment; 2. *G. obtusata* (Sol.), Lamx., fragment; 3. *Eucheuma Cottonii*, n. sp.; 4. *Fauchea microspora*, Born.; 5. *Gloioderma* (?) *expansa*, n. sp.; 6. *Chylocladia perpusilla*, n. sp.; 7. *Dictyurus purpurascens*, Bory; 8. *Cryptonemia seminervis*, J. Ag.; 9. *Cryptonemia* spec.; 10. *Peyssonnelia coccinea*, J. Ag.; 11. *P. Harveyana* (?), Crouan; 12. *Cruoriopsis cruciata*, Duf.

Cargados Carajos.

1. *Gloiophlœa articulata*, n. sp.; 2. *Iridæa* spec., fragment; 3. *Eucheuma Cottonii*, n. sp.; 4. *Dasyopsis Stanleyi*, n. sp.; 5. *D. Geppii*, n. sp.; 6. *Heterosiphonia Rendlei*, n. sp.; 7. *Dictyurus purpurascens*, Bory; 8. *Haloplegma Preissii*, Sond.; 9. *Ceramium* spec.

III. Systematic Survey of all the Algæ collected by Mr. J. Stanley Gardiner in the Indian Ocean.

Family.	Locality.	Reef or Lagoon.	Depth.	Distribution.
Helminthocladiaceæ.				
1. *Chantransia Liagoræ*, n. sp.	Coetivy.	Reef.		
1. *Liagora orientalis*, J. Ag.	Coetivy.	Reef.	.....	Indian Ocean, Ceylon.
2. *Liagora hawaiiana*, Butt.	Coetivy.	Reef.	.....	Pacific Ocean, Laie Point, Koolauloa, Oahu.
1. *Dermonema dichotomum*, Harv.	Mahé, Terné.	Reef.	.....	Ceylon, Malay Archipelago, Formosa.
Chætangiaceæ.				
1. *Gloiophlœa* (?) *articulata*, n. sp.	Cargados Carajos.	.....	30–45 fms.	
1. *Galaxaura Liebmanni* (Ar.), Kjellm....	Praslin.	Reef.	.....	Gulf of Mexico.
2. *Galaxaura hawaiiana*, Butt.	Aldabra.	Passe Houareau, outside.	.....	Pacific Ocean, French Frigate Shoal, Bird Island.
3. *Galaxaura fastigiata*, Decne.	Mahé, Terné.	Reef.	.....	Pacific Ocean, Philippines; Malay Archipelago.
	Saya de Malha.	.....	Over 26 fms.	
4. *Galaxaura veprecula*, Kjellm.	Amirante.	.....	20–25 fms.	Indian Ocean, Madagascar.
5. *Galaxaura obtusata* (Sol.), Lamx.	Saya de Malha.	.....	26 fms.	Warm Atlantic, West Indies; Pacific Ocean, Loo Choo Isl., Japan.

Family.	Locality.	Reef or Lagoon.	Depth.	Distribution.
Gelidiaceæ.				
1. *Gelidium crinale* (Turn.), Lamx.	Diego Garcia.	Reef.	.....	Mediterranean; Red Sea.
2. *Gelidium pannosum*, Grun.	Coetivy.	Reef.	.....	Ceylon, Friendly Islands, Fiji, Tonga, and Samoa Islands.
Gigartinaceæ.				
1. *Iridæa* spec., ♀	Cargados Carajos.	.....	22 fms.	
	Amirante.	.....	20–25 fms.	
1. *Polycœlia van Hoevellii*, n. sp.	Amirante.	.....	30–100 fms.	Malay Archipelago.
Rhodophyllidaceæ.				
1. *Sarconema furcellatum*, Zan.	Seychelles, Long Isl.	Reef.	.....	Red Sea; Indian Ocean.
1. *Eucheuma Cottonii*, n. sp.	Cargados Carajos.	.....	26 fms.	Many species of *Eucheuma* occur on the east coast of Africa.
	Saya de Malha.	.....	25 fms.	
Sphærococcaceæ.				
1. *Gelidiopsis variabilis* (Grev.), Schm.	Seychelles, Long Isl.	Reef.	..	Indian Ocean, east coast of Africa.
2. *Gelidiopsis rigida* (Vahl), Web. v. B.	Seychelles, Praslin	Reef.		Tropical seas.
	Diego Garcia.			
	Mahé, Terné.			
1. *Gracilaria compressa* (Ag.), Grev.	Amirante.	.....	25 fms.	Atlantic Ocean; Mediterranean; Gulf of Mexico.
1. *Corallopsis Cacalia*, J. Ag.	Mahé, Terné.	Reef.	.....	Red Sea, east coast of Africa.
	Seychelles, Long Isl.	Reef.		
1. *Calliblepharis prolifera* (Harv.), J. Ag.	Amirante.	.....	25 fms.	New Zealand.
1. *Hypnea divaricata* (?), Grev.	Aldabra.	Lagoon.	.....	Gulf of Mexico; Pacific, Tongatabu.
2. *Hypnea Valentiæ* (Turn.), Mont.	Seychelles, Long Isl.	Reef.	.....	Red Sea; Indian Ocean; Port Denison.
3. *Hypnea pannosa*, J. Ag.	Chagos Archipelago.	Lagoon.	.....	Coast of Mexico; Mauritius; Ceylon; Tonga Archipelago; New Caledonia.
	Aldabra.	Reef.		
	Seychelles.	Reef.		
	Praslin.	Reef.		
	Mahé, Terné.	Reef.		
4. *Hypnea* spec.	Amirante.	.....	25 fms.	
Rhodymeniaceæ.				
1. *Fauchea microspora*, Born.	Saya de Malha.	.....	53 fms.	Mediterranean.
1. *Gloioderma* (?) *expansa*, n. sp.	Saya de Malha.	.....	53–55 fms.	
1. *Champia compressa*, Harv.	Amirante.	.....	20–25 fms.	Cape of Good Hope; Malay Archipelago; Pacific Ocean.
	Coetivy.	Reef.		
2. *Champia* spec.	Seychelles, Long Isl.	Reef.		
1. *Chylocladia perpusilla*, n. sp.	Saya de Malha.	.....	29 fms.	
1. *Cœlarthrum Albertisii* (Picc.), Börg.	Amirante.	.....	20 fms.	Canary Islands; Bermudas; Malay Archipelago.
Delesseriaceæ.				
1. *Hypoglossum* spec.	Amirante.	.....	35 fms.	
1. *Nitophyllum* spec.	Amirante.	.....	25 fms.	
Rhodomelaceæ.				
1. *Laurencia nidifica*, J. Ag.	Aldabra.	Reef.	.. ..	Sandwich Islands; Malay Archipelago.
2. *Laurencia obtusa* (Huds.), Lamx.	Aldabra.	Reef.	.....	Mediterranean; Fiji Islands; Malay Archipelago.
	Coetivy.			
	Egmont.			
3. *Laurencia papillosa* f. *australica*	Aldabra.	Reef.	.....	New Caledonia.
	Coetivy.	Reef.		
	Seychelles, Long Isl.	Reef.		
4. *Laurencia spinulifera*, Kütz.	Chagos Arch., Diego Garcia.	Reef.	.. ..	Indian Ocean.
5. *Laurencia pygmæa*, n. sp.	Chagos Arch., Diego Garcia.	Reef.		
6. *Laurencia ceylanica*, J. Ag.	Amirante.	.....	20 fms.	Ceylon; Malay Archipelago.
	Coetivy.	Reef.		
1. *Acanthophora orientalis*, J. Ag.	Mahé, Terné.	Reef.	.....	Zanzibar; Malay Archipelago; North Australia; Tonga Archipelago; Marianne Islands.
	Seychelles, Long Isl.	Reef.		
1. *Pseudendosiphonia Gardineri*, n.g., n.sp.	Amirante.	.....	25 fms.	
1. *Cladhymenia oblongifolia*, Hook. et Harv.	Amirante.	.....	25 fms.	New Zealand.
1. *Chondria pumila*, Vick.	Chagos Arch., Diego Garcia.	Reef.	.....	Barbados.
2. *Chondria simpliciuscula*, n. sp.	Aldabra.	Reef.		

Family.	Locality.	Reef or Lagoon.	Depth.	Distribution.
Rhodomelaceæ (*con.*).				
1. *Polysiphonia* spec.	Praslin.	Reef.		
1. *Roschera glomerulata* (Ag.), n. comb.	Seychelles, Long Isl.	Reef.	....	Zanzibar; Indian Ocean; Malay Archipelago.
1. *Herposiphonia prorepens* (Harv.), Schm.	Chagos Arch.	.....	.	Algoa Bay; Western Australia.
1. *Oligocladus Prainii*, n. sp.	Coetivy.	Reef.		
2. *Oligocladus pusillus*, n. sp.	Coetivy.	Reef.		
1. *Dasyopsis Stanleyi*, n. sp.	Cargados Carajos.	.....	30 and 47 fms.	
2. *Dasyopsis aperta*, n. sp.	Coetivy.	Reef.		
	Cargados Carajos.	.....	47 fms.	
3. *Dasyopsis Geppii*, n. sp.	Amirante.	.....	20–25 fms.	
	Cargados Carajos.	.....	25 fms.	
	Coetivy.	Reef.		
	Chagos Arch.			
4. *Dasyopsis palmatifida*, n. sp.	Amirante.	.....	20–25 fms.	Malay Archipelago.
	Coetivy.	Reef.		
	Chagos Arch.			
1. *Tapeinodasya Ethelæ*, n. sp.	Amirante.	.....	20–25 fms.	
1. *Heterosiphonia Rendlei*, n. sp.	Cargados Carajos.	.....	47 fms.	
2. *Heterosiphonia* spec.	Coetivy.	Reef.		
1. *Dictyurus purpurascens*, Bory	Saya de Malha.	Reef.	55 fms.	Cape Comorin; Indian Ocean, Mauritius, Ceylon; Malay Archipelago; Diego Garcia.
	Coetivy.		30 fms.	
	Amirante.		30 and 47 fms.	
	Cargados Carajos.		22 fms.	
	Chagos Arch., Salomon.			
1. *Amphisbetema indica* (J. Ag.)	Aldabra.	Reef.	.....	Diego Garcia.
Ceramiaceæ.				
1. *Griffithsia* spec.	Amirante.	.....	20–25 fms.	
1. *Haloplegma Preissii*, Sond.	Cargados Carajos.	.....	20, 30, and 47 fms.	Western Australia, Tasmania; Malay Archipelago.
1. *Antithamnion adnatum*, J. Ag.	Salomon.	Reef.	.....	New Zealand; Malay Archipelago.
1. *Spyridia filamentosa* (Wulf.), Harv.	Aldabra.	Reef.	.....	Mediterranean; Red Sea; Dar-es-Salaam; Malay Archipelago; West Indies.
1. *Ceramium cinnabarinum* (Gratel.), Hck.	Salomon.	.....	.....	Mediterranean; Malay Archipelago.
2. *Ceramium* spec.	Cargados Carajos.	.....	47 fms.	
1. *Reinboldiella Schmitziana* (Rbd.), de Toni.	Chagos Arch., Egmont, Salomon.	Reef.	.....	Japan; Malay Archipelago.
Grateloupiaceæ.				
1. *Halymenia polyclada*, A. & E. S. Gepp, var. *aldabradensis*, n. v.	Aldabra.	Outer reef.		
1. *Cryptonemia seminervis*, J. Ag.	Amirante.	.....	20–25 fms.	Atlantic; Mediterranean; Red Sea.
	Saya de Malha.	.....	55 fms.	
2. *Cryptonemia* spec.	Saya de Malha.	.....	55 fms.	
Squamariaceæ.				
1. *Peyssonnelia coccinea*, J. Ag.	Seychelles.	.....	31 fms.	West coast of Australia; Malay Archipelago.
	Saya de Malha.	.....	55 fms.	
2. *Peyssonnelia Harveyana* (?), Crouan	Saya de Malha.	.....	55 fms.	Coast of France near Brest.
3. *Peyssonnelia calcea*, Heydr.	Egmont.	Reef.	.....	Tami, near German New Guinea; Malay Archipelago.
	Peros, Coin.			
4. *Peyssonnelia polymorpha* f. *Gardineri*, n. f.	Amirante.	.....	30, 45–60 fms.	
5. *Peyssonnelia biradiata*, n. sp.	Seychelles.	.....	31 fms.	Malay Archipelago.
6. *Peyssonnelia* spec.	Saya de Malha.			
1. *Cruoriopsis cruciata* (?), Duf.	Saya de Malha.	.....	29 fms.	Adriatic; Malay Archipelago.
Corallinaceæ.				
1. *Melobesia callithamnioides*, Falk.	Egmont.	Reef.	.....	Atlantic (?); Mediterranean.
1. *Amphiroa fragilissima*, Lamx.	Chagos Arch.	Reef.	.....	West Indies; Pacific; Malay Archipelago; Dar-es-Salaam.
	Mahé, Cap Terné.	Reef.		
2. *Amphiroa foliacea*, Lamx.	Praslin.	Reef.	.....	Marianne Islands; Malay Archipelago.
1. *Jania tenella*, Kütz.	Coetivy.	Reef.	.....	Malay Archipelago; Gulf of Mexico.
	Seychelles.	Reef.		
	Peros, Coin.	Reef.		
	Praslin.	Reef.		
	Mahé, Cap Terné.	Reef.		

IV. Systematic Account.

Fam. HELMINTHOCLADIACEÆ.

Chantransia (DC.), Schmitz.

1. Chantransia Liagoræ, n. sp.

Thallo endophytico et epiphytico, nano, cæspitibus globosis sparsis Liagoræ insidente, constante e filis hospitem intrantibus et filis erectis. Filis erectis parce ramosis, ramis post monosporangia terminalia delapsa egredientibus; pilis non visis, verisimiliter raris. Monosporangiis aut terminalibus aut lateralibus, pedicello ramoso suffultis, ramis denuo monosporangia ferentibus. Filis latis 6–8–12 μ, articulis 16–20 μ longis. Monosporangiis non maturis; antheridiis et carpogoniis non visis.

Coetivy, reef, on *Liagora hawaiiana*; in alcohol.

This little *Chantransia* forms a small tuft, which penetrates between the horizontal filaments of the *Liagora* and attaches itself at their base. I could detect no creeping filaments in the host plant giving rise to new tufts. It has a height of 1 mm., the axes are sparingly and irregularly branched and bear monospores both at the apex and laterally. After the monospore has fallen off, or perhaps while still *in situ*, the filament or branch that carries it grows out sideways. I also noted clusters of carpospores; these are not arranged in series as in *C. efflorescens*. The filaments have a breadth of 6–8, rarely of 12 μ, and their cells a length of up to 20 μ. On account of the algæ having been first preserved in formalin and afterwards in alcohol, it is difficult to judge the shape of the chromatophore.

I believe that this alga is a new species; there are, so far as I know, only two other species of *Chantransia* on *Liagora*, namely, *Ch. Barbadensis* and *Ch. Nemalionis*, which were found on *Liagora elongata* by Miss Vickers. Our alga differs from both species in the smaller size of its cells and filaments.

Liagora, Lamouroux.

1. Liagora orientalis, J. Ag.

J. Agardh, Analecta algologica, 1896, p. 99.

Coetivy, reef; in alcohol.

Distribution. Indian Ocean, Ceylon.

2. Liagora hawaiiana, Butt.

Butters, "*Liagora* and *Galaxaura*," Minnesota Bot. Studies, vol. iv. part 2, 1911, p. 169.

Coetivy, reef; in alcohol.

Distribution. Laie Point, Koolauloa, Oahu, Pacific Ocean.

Liagora hawaiiana belongs to the group of *Liagoræ* with dichotomously branched fronds. It differs from all known species of this group in having an articulate frond; at the top of the thallus the articulations are inconspicuous, but lower down they are

very distinct. The articulations are at the base of each dichotomy and the internodes are as a rule long.

Dermonema, Greville.

1. Dermonema dichotomum, Harv.

Harvey, Ceylon Algæ, n. 93.
Schmitz u. Hauptfleisch in Engler u. Prantl, Natürl. Pflanzenfam., Teil 1, Abt. 2, 1896, p. 335.
De Toni, Syll. Alg. vol. iv. sect. i. 1897, p. 102.

Terné Mahé; dry specimens.

Distribution. Ceylon; Formosa; Malay Archipelago.

Fam. CHÆTANGIACEÆ.

Gloiophlœa, J. Agardh.

1. Gloiophlœa (?) articulata, n. sp. (Plate 12. fig. 1; Plate 14. figs. 26, 27.)

Frondibus dichotomis, articulatis, usque ad 18 cm. altis, ramulos adventitios ex nodis orientes gerentibus; internodiis cylindraceis, subcompressis, ad basin contractis; internodio terminali apice rotundato. Frondibus constantibus e cylindro centrali filis hyalinis, tenuibus, peripheriam versus excurrentibus contexto. Filis per dichotomiam divisis, stratum peripheric um cellularum minimarum moniliformium arcte conjunctarum et cuticula crassa coopertarum formantibus. Organis generationis ignotis.

Cargados Carajos, dry specimen, 30 fms.; in alcohol, 45 fms.

The algæ from Cargados Carajos are barren, the determination is therefore not beyond doubt, but the anatomical structure of these plants is so typical and so like that of the family Chætangiaceæ (Pl. 14. figs. 26, 27) that I should be very much surprised if the organs of fructification should prove these algæ to belong to another family. Amongst the Chætangiaceæ they stand nearest to *Gloiophlœa*. They are distinguished, however, from *Gloiophlœa scinaioides*—the only known species of the genus—by their articulate frond; the internodes are usually—though not always—contracted into a short pedicel-like node, and from this node adventitious branches may spring, but as a rule the branching is dichotomous. The peripheral layer consists of small cortical cells, covered by a rather thick cuticle; these small tightly adhering cortical cells distinguish the genus *Gloiophlœa* from the genus *Scinaia*.

Galaxaura, Lamouroux.

1. Galaxaura Liebmanni (Aresch.), Kjellm.

Areschoug, Phyceæ novæ, in Act. Reg. Soc. Scient. Upsal. ser. 3, vol. i. 1854, p. 356.
Kjellman, "Floridé Slägtet *Galaxaura*," in Kongl. Sv. Vet.-Akad. Handl. Bd. xxxiii. 1900, p. 46.

Praslin, reef; in alcohol.

Distribution. Mexico; Vera Cruz.

Though *Galaxaura Liebmanni* is only known from the West Indian tropical seas, the peculiar structure of the short cortical filaments and the compact outward appearance

of the algæ from Praslin seem to indicate that they belong to *G. Liebmanni* rather than to *G. collabens* from Australia, described by Kjellman as "solitaria, erecta et robusta." The plants from Praslin are short, intricate, and grow close together; the short cortical filaments consist, as a rule, of four cells only, and of these the lower one is by far the largest.

2. GALAXAURA HAWAIIANA, Butt. (Plate 13. fig. 25.)

Butters, "*Liagora* and *Galaxaura*," Minnesota Bot. Studies, vol. iv. part 2, 1911, p. 176.

Aldabra, reef, outside Passi Honakan.

Distribution. Pacific Ocean, French Frigate Shoal, Bird Island.

The algæ from Aldabra are very much like *Galaxaura hawaiiana*, Butt., and the differences between the description of *G. hawaiiana* (I have seen no type specimen) and the algæ from Aldabra are not, I think, sufficiently great to warrant the description of a new species. The algæ from Aldabra are a little longer (they have a length of 7 cm., a breadth of 2 mm.), and the long internodes are not tapering, but rounded or truncate. The frond is slightly but distinctly annulate, and in the dried specimens of a remarkable dark brown-red colour; the anatomical structure is like that of *G. hawaiiana*, Butt. Butters records *G. hawaiiana* from depths of 14–16 and 26 fathoms; the specimens from Aldabra were found at the outside of Passi Honakan. This difference of locality may perhaps account for the small differences observable in the two plants. I have given a figure of the Aldabra plant, which shows very well the long terminal internodes.

3. GALAXAURA FASTIGIATA, Decne.

Decaisne, Sur les Corallines, 1842, p. 16.
Kjellman, "Floridé Slägtet *Galaxaura*," in Kongl. Sv. Vet.-Akad. Handl. Bd. xxxiii. 1900, p. 64.

Terné Mahé; dry specimen.
Saya de Malha; fragment only.
Distribution. Pacific Ocean; Philippines; Malay Archipelago.

4. GALAXAURA VEPRECULA, Kjellm.

Kjellman, "Floridé Slägtet *Galaxaura*," in Kongl. Sv. Vet.-Akad. Handl. Bd. xxxiii. 1900, p. 80.

Amirante, 20–25 fms.; in alcohol.
Distribution. Indian Ocean, Madagascar.

5. GALAXAURA OBTUSATA (Sol.), Lamx.

Solander in Ellis, Zoophytes, 1786, p. 113.
Lamouroux, Polypiers coralligènes, 1816, p. 262.
Agardh, Epicrisis systematis Floridearum, 1876, p. 525.

Saya de Malha, 26 fms.; only a small specimen.
Distribution. Warm Atlantic, West Indies; Pacific Ocean, Loo Choo Islands, Japan.

Fam. GELIDIACEÆ.

Gelidium, Lamouroux.

1. Gelidium crinale (Turn.), Lamx.

De Toni, Syll. Alg. vol. iv. sect. i. 1897, p. 146.
Fucus crinalis, Turner, Hist. Fuc. tab. 198.

Chagos Archipelago, Diego Garcia, in alcohol; no indication of depth.
Distribution. Mediterranean; Red Sea.

2. Gelidium pannosum, Grun.

Grunow, Algen der Fiji, Tonga u. Samoa Inseln, 1874, p. 40.

Coetivy, reef, on a piece of coral; in alcohol.
Distribution. Upolu, Samoa Archipelago; Ceylon; Friendly Islands.

Fam. GIGARTINACEÆ.

Iridæa, Bory.

1. Iridæa spec.

Cargados Carajos, fragment with cystocarps, in alcohol, 22 fms.
Amirante, fragment with tetraspores, in alcohol, 20–25 fms.

The specimens from both localities are too fragmentary to allow of a specific determination, though the tetraspores being scattered among the peripheral cells indicate that the plant belongs to the subgenus *Rhodoglossum*, J. Ag. Both specimens are so alike in anatomical structure and outward appearance that, as far as can be judged from the small fragments, I feel almost certain that they belong to the same species.

Polycœlia, J. Agardh.

1. Polycœlia van Hœvellii, n. sp.

Amirante, 30–100 fms.; in alcohol.
Distribution. Malay Archipelago.

The species is represented in the collection by such a poor and barren fragment that I should have been unable to name it, had it not been for my studies on the rich material collected during the 'Siboga' Expedition in the Malay Archipelago. This alga will therefore be described and figured in the forthcoming paper on the 'Siboga' algæ.

Fam. RHODOPHYLLIDACEÆ.

Sarconema, Zanardini.

1. Sarconema furcellatum, Zan.

Zanardini, Plantæ Mar. Rubro Enum. p. 264.
De Toni, Syll. Alg. vol. iv. sect. i. 1897, p. 367.

Seychelles, Long Island.
Distribution. Red Sea; Indian Ocean.

Eucheuma, J. Agardh.

1. Eucheuma Cottonii, n. sp. (Plate 12. fig. 2.)

Thallo crasso, carnoso, depresso, decumbente, lateraliter et subdichotomice ramoso, latere superiore verrucis et tuberculis aggregatis, latere inferiore tuberculis remotioribus obsito. Verrucis nonnunquam forma irregulari; tuberculis vulgo parvis et rotundis, nonnunquam apiculatis. Regione mediana thalli ad apices e cellulis satis magnis hyphis circumdatis constante, hyphis infra item auctis et cellulas satis magnas formantibus; peripheriam versus cellulis diminutis et ibidem series breves formantibus. Organis fructificationis ignotis.

Saya de Malha, 25 fms.; in alcohol.

Cargados Carajos, 26 fms.; dry specimen.

E. Cottonii is unfortunately a barren plant, and shows, in a dry state, a great likeness to species of *Gracilaria*. I moistened it, to restore as much as possible its natural appearance, and was then struck by its great resemblance to *Eucheuma*. The figures are made from these moistened specimens, and show well the horizontally spread, laterally branched thallus, covered with warts and more or less pointed tubercles. The anatomical structure at the apex is also entirely different from that of *Gracilaria*, though, in a cross-section at some distance from the apex, only round, rather large, and somewhat thick-walled cells are to be seen. But these cells are of different origin to the primary large cells, for at the apex the latter are seen to be surrounded by narrow hyphæ, which grow out lower down into large cells and are then no longer discernible as hyphæ.

The genus *Eucheuma* is described by Schmitz in Engler u. Prantl, 'Pflanzen-Familien,' as having a central axis of slender elongated hyphæ. This axis is found, for instance, in *E. spinosum*. Agardh has, however, called attention to the fact that *E. Schrammi* has a structure in which "fila strati interioris sparsim inter cellulas strati intermedii quasi introducta obveniunt." Schmitz, again, supposes that *E. Schrammi*, Crouan, is not an *Eucheuma* but an *Euryomma*.

My studies on the *Eucheumata* of the Malay Archipelago seem to indicate that there are species of *Eucheuma* without a central axis of longitudinal hyphæ. The investigations are not complete, but it appears to me not improbable that the cylindrical erect species have an axis of narrow cells, and that in the flat prostrate species this is absent. I did not find an axis in any prostrate specimens of *Eucheuma* of which I was able to study the cystocarp. The whole question needs to be further investigated, but for the present it seems highly probable that the algæ from Saya de Malha and Cargados Carajos belong to the genus *Eucheuma*, and the name I propose for it is in kind remembrance of Mr. Cotton's friendly help.

Fam. SPHÆROCOCCACEÆ.

Gelidiopsis, Schmitz.

1. Gelidiopsis variabilis (Grev.), Schmitz.

Schmitz, Marine Florideen von Deutsch Ost-Afrika, in Engler's Bot. Jahrb. Bd. xxi. H. 1, 2, 1895, p. 148.

Seychelles, Long Island, reef.

Distribution. Indian Ocean; East coast of Africa.

2. Gelidiopsis rigida (Vahl), Web. v. B.

Recueil des Travaux botaniques Neérlandais, no. 1, 1905, p. 9.
Fucus rigidus, Vahl, in Naturh. Sellskabets Skrifter, v. p. 46.

Seychelles, reef; dry specimen.
Praslin, reef; dry specimen and in alcohol.
Diego Garcia, reef; dry specimen.
Terné Mahé, reef; dry specimen.
Distribution. Common in tropical seas.

In 1904 I wrote in the above-mentioned paper that it appeared to me that the well-known *Gelidium rigidum* of the tropical seas was not a *Gelidium*, but belonged to the genus *Gelidiopsis*. In 1909 Prof. Okamura gave, in his 'Icones of Japanese Algæ,' pl. lix., a figure of this alga and also of its large apical cell, and named it *Gelidium rigidum*. I had failed to detect this large apical cell, and its absence was one of the reasons why I thought that the alga could not be a *Gelidium*; I had seen no cystocarps. Quite recently, in 'Icones of Japanese Algæ,' vol. ii. No. 10, p. 188, Prof. Okamura has recalled his statement, made before he had seen my paper, and agrees with me in naming *Gelidium rigidum*, *Gelidiopsis rigida*. This alga varies in its ramification, the lateral branches being short or long, or sometimes unilaterally inserted. I believe, however, that these variations are only a form of growth.

Gelidiopsis being a feminine substantive in the Greek language, the adjective should have the feminine ending, and I made an error when I called the alga *Gelidiopsis rigidum* in 1904.

Gracilaria, Greville.

1. Gracilaria compressa (Ag.), Grev.

Agardh, Species Algarum, 1823, p. 308.
Greville, Algæ Britann. 1830, p. 125.
De Toni, Syll. Alg. vol. iv. sect. ii. 1900, p. 438.

Amirante, 25 fms.
Distribution. Atlantic Ocean; Mediterranean; Gulf of Mexico.
The specimen is rather slender for *G. compressa* and scantily branched, but I assume

that the great depth at which it was gathered may in some measure account for this. It bears cystocarps, and these have a little funnel at the top, exactly as in *G. compressa*.

Corallopsis, Greville.

1. Corallopsis Cacalia, J. Ag.

J. Agardh, Epicrisis systematis Floridearum, 1876, p. 409.
De Toni, Syll. Alg. vol. iv. sect. II. 1900, p. 459.

Terné Mahé; dry specimens.
Seychelles, Long Island; dry specimens.
Distribution. Red Sea.

The specimens of the Seychelles are more branched than those of Terné Mahé, still I believe that they belong to the same species; some branches recall those of *C. minor*.

Calliblepharis, Kützing.

1. Calliblepharis prolifera (Harv.), J. Ag. (Plate 12. fig. 3.)

Epicrisis systematis Floridearum, 1876, p. 432.
Rhodymenia prolifera, Harvey, in Flora Nova-Zeelandia, p. 249.

Amirante, 25 fms.; dry specimens.
Distribution. New Zealand.

Harvey described this alga under the name of *Rhodymenia prolifera*, but J. Agardh pointed out that the structure of the cystocarp was unlike that of *Rhodymenia* and similar to that of *Calliblepharis*. The alga differs, however, from the other species of this genus in bearing the cystocarps on the broad part of the thallus and not on special leaflets; Agardh called it therefore *Calliblepharis? prolifera*. As the specimens from Amirante were fertile, I studied the ripe cystocarps; they have the same structure as those of *Calliblepharis*, and I do not think that the absence of special leaflets should be a reason to maintain J. Agardh's note of interrogation.

It is remarkable to find *Calliblepharis prolifera* in Mr. Stanley Gardiner's collection, since it had previously only been found in New Zealand.

Hypnea, Lamouroux.

1. Hypnea (divaricata ?), Grev.

Greville, Alg. Brit. p. lix.
De Toni, Syll. Algarum, vol. iv. sect. II. 1900, p. 478.

Aldabra, fragment only, lagoon; dry specimen.
Distribution. Gulf of Mexico; Mascarenes (?); Tongatabu.

As far as I could judge by the small fragment, the specimen belonged to *H. divaricata*, Grev. It differed from *H. Valentiæ* in the absence of small stellate spines.

2. Hypnea Valentiæ (Turn.), Mont.

Cryptog. Canar. p. 161.
De Toni, Syll. Algarum, vol. iv. sect. ii. 1900, p. 479.
Fucus Valentiæ, Turner, Historia Fucorum, 1809, tab. 78.

Seychelles, Long Island; dry specimen.
Distribution. Red Sea, Indian Ocean; Port Denison.

3. Hypnea pannosa, J. Ag.

J. Agardh, Alg. Liebman, p. 14.
Grunow, Algen der Fiji, Samoa u. Tonga Inseln, 1874, p. 39.

Aldabra; dry specimen.
Seychelles, reef; dry specimen.
Praslin; in alcohol.
Chagos Archipelago, Coin Peros, lagoon; in alcohol.
Terné Mahé, reef; dry specimen.
Distribution. Coast of Mexico; Mauritius; Ceylon; Tonga Archipelago; New Caledonia.

Among the specimens from Praslin were some overgrown by a sponge; the branches thus hemmed in were obviously less branched and more cylindrical than the free-growing ones. The specimens from Terné Mahé are exactly like those from Mexico in Kützing's herbarium and figured in Tab. Phyc., Band xviii. tab. 27. The specimens from the other localities are like those gathered by Harvey at the Friendly Islands, No. 44, and by Schmarda on the west coast of Ceylon. There is a difference between Harvey's and Schmarda's specimens, but both being barren I abstained from further examination.

4. Hypnea spec.

Amirante, 25 fms.
An indeterminable specimen, altered perhaps a little in consequence of the great depth at which it grew.

Fam. RHODYMENIACEÆ.

Fauchea, Montagne et Bory.

1. Fauchea microspora, Born.

Bornet in Rodriguez, Algas de las Baleares, 1889, p. 253, et in Bull. Soc. Bot. t. xxxvii. 1890, p. 142.

Saya de Malha, 53 fms.; dry specimens.
Distribution. Mediterranean.
The plants are all barren, but the whole outward appearance of these algæ corresponds so well with the description given by Borret that I feel no doubt that they belong to this species.

Gloioderma, J. Agardh.

1. Gloioderma (?) expansa, n. sp. (Plate 14. figs. 28, 29.)

Thallo membranaceo, plano, verisimiliter horizontaliter expanso, margine proliferationibus in thallos juveniles excrescentibus. Thallo sæpe anastomosante, constante e strato unico cellularum maximarum centralium, utroque latere duobus stratis cellularum parvarum et uno strata cellularum minimarum periphericarum cincto. Cystocarpiis et antheridiis ignotis; tetrasporangiis in strato corticali parum mutato dispersis, cruciatis divisis.

Saya de Malha, 53–55 fms.; dry specimens.

This alga seems to be new to science, and I have referred it to the family of the Rhodymeniaceæ on account of its large central cells placed in one series only. Its outward appearance recalls *Rhodophyllis peltata*, Grun., of the Tonga Archipelago, but it differs from that alga in having only one series of large central cells, whilst all species of *Rhodophyllis* have two series. Amongst the Rhodymeniaceæ it belongs, I think, to the genus *Gloioderma*, because it has very small peripheral cells and cruciate tetrasporangia scattered in the cortical layer, which is, nevertheless, very little changed.

Unfortunately I have seen neither procarps, cystocarps, nor antheridia, and therefore the generic position of the alga remains uncertain. It needs to be further investigated, for it was gathered at a great depth (53–55 fms.), from which few Rhodophyceæ are known.

By its broad, membranous, unbranched frond, which bears excrescences along its margin, and sometimes, though rarely, on the frond itself, this alga is easily distinguished from all other species of *Gloioderma*, as these have mostly a dichotomous or pinnate ramification. The entirely different mode of growth of the alga from Saya de Malha, and the great depth at which it was gathered, almost suggest that it may be the type of a new genus.

Champia, Desvaux.

1. Champia compressa, Harv.

Harvey, Genera South African Plants, ed. 1, p. 402.

De Toni, Syll. Alg. vol. iv. sect. II. p. 561.

Amirante, 20–25 fms.; small fragment, in alcohol.

Coetivy, reef; dry specimen.

Distribution. Cape of Good Hope; Ceylon; Malay Archipelago; Friendly Islands; Australia (?); New Caledonia.

2. Champia spec.

Seychelles, Long Island, reef; dry specimen.

A small specimen intermingled with *Gelidiopsis variabilis*. The simple main axis bears a few short branches, irregularly placed. Several main branches have grown

together, and cannot be separated without damage. The plant has distinct inflated articulations blunt at both sides, and is certainly different from *Champia compressa*. It strongly recalls *Ch. parvula*, especially the figure given by Kützing in his Tab. Phyc., Band xv. tab. 89, where *Ch. parvula* is figured under the name of *Lomentaria intertexta*. The plant from the Seychelles is, however, very small, having a height of only 1 cm., and it is barren.

Chylocladia, Greville.

1. Chylocladia perpusilla, n. sp. (Plate 12. figs. 4, 5.)

Thallo minusculo, decumbente, ramuloso, cavo, sine diaphragmate; ramo primario interne multis cellulis magnis; ramulis constantibus e strato unico peripherico cellularum magnarum et parvarum secundum quarum latus interne fila ramosa decurrunt, nonnunquam glandulas ferentia. Sporangiis in ramulorum dilatatorum, cavitatem prominentibus, nec in cavernis propriis sitis. Cystocarpiis et antheridiis ignotis. Thallo lato 0·5–0·6 m.

Saya de Malha, creeping on *Udotea*, 29 fms.

This tiny plant was found creeping on *Udotea*, though it did not appear to possess rhizoids. It has a main axis, from which spring slender ramuli, sometimes opposite, but mostly irregular; the specimen is, however, so small that it is impossible to say much as to its ramification. The main axis has a length of 1 cm. and a breadth of 600 μ, the branches have a length of 2–5 mm. The branches are entirely hollow, but the downgrowing filaments that are proper to the genus bear glands (?); the main axis is filled with large cells, loosely attached to one another. I could see no diaphragms, neither in the branches nor at the base of the branches; the tetraspores are scattered over the inflated top of some branches; they protrude into the cavity of the branch, but they are not situated in a special hollow, as they are in *Lomentaria*.

On account of the position of the tetraspores and the absence of diaphragms, I believe that this little plant belongs to the genus *Chylocladia*. Its small size characterizes it as a new species.

Cœlarthrum, Börgesen.

1. Cœlarthrum (Albertisii ?) (Picc.), Börg.

"Some new or little-known West Indian Florideæ, II.," in Bot. Tidsskr. Bd. xxx. 1910, p. 189.
Lomentaria Albertisii, Piccone, Alghe in "Crociera del Corsaro," 1884, p. 37.

Amirante, 20 fms.; dry specimen.

Distribution. Canary Islands; Guadeloupe and Bermudas; West Indies; Malay Archipelago.

I think it very probable that the alga from Amirante is *Cœlarthrum Albertisii*, because I found that species amongst the 'Siboga' material. I cannot deny, however, that the specimen has smaller articulations than the type and that I did not see in my

preparations the peculiar glands described by Mr. Börgesen. In how far, however, these differences may depend upon the depth at which the plant was gathered, I do not venture to say. The specimen—and it is only a fragment—gives the impression of being still very young and therefore I wish to be doubly cautious in my opinion as to it.

Fam. DELESSERIACEÆ.

Hypoglossum, Kützing.

1. Hypoglossum spec.

Amirante, 25 fms.; dry specimen.

A fragment; probably *Hypoglossum spathulatum* (Kütz.), J. Ag. (*Delesseria hypoglossoides*, Harvey, Austral. Alg.), but the specimen is too badly preserved to be identified with certainty.

Nitophyllum, Greville.

1. Nitophyllum spec.

Amirante, 25 fms.

Only a poor fragment, attached to other algæ and indeterminable, but with a tetraspore-bearing sorus typical for this genus.

Fam. RHODOMELACEÆ.

Subfam. Laurencieæ.

Laurencia, Lamouroux.

1. Laurencia nidifica, J. Ag.

J. Agardh, Spec. Alg. ii. 1863, p. 749.
De Toni, Syll. Alg. vol. iv. sect. iii. 1903, p. 785.

Aldabra, reef.

Distribution. Sandwich Islands; Malay Archipelago.

2. Laurencia obtusa (Huds.), Lamx.

Essai de classification, p. 42.
De Toni, Syll. Alg. vol. iv. sect. iii. 1903, p. 791.
Fucus obtusus, Hudson, Flora Anglica, ed. iii. p. 586.

Aldabra, reef; dry specimens.

Coetivy, reef; dry specimen.

Egmont, reef and shoal; in alcohol.

Distribution. Mediterranean; Fiji Islands; Malay Archipelago.

Laurencia obtusa is represented by two forms in the Stanley Gardiner collection; from Aldabra there are three packets (nos. 4, 5, 8). No. 4 is the stoutest plant, no. 5 and

no. 8 are more slender, while the alga from Coetivy Reef is very much like specimens in Kützing's herbarium and named *L. obtusa* var. *racemosa*. The specimens from Egmont Reef are rather short, but they probably represent young plants. They show the characteristic branching of the species, and all the branches have blunt truncated apices.

3. Laurencia papillosa (Forsk.), Grev., f. australica, in herb. Kützing.

Aldabra, reef; dry specimen.
Seychelles, Long Island; dry specimen.
Distribution. New Caledonia.

I have been in doubt about these algæ for they differ from typical specimens of *L. papillosa*. They come near to two barren specimens from New Caledonia in Kützing's Herbarium. Mr. Stanley Gardiner's specimens being also barren, I abstained from giving a diagnosis.

4. Laurencia spinulifera, Kütz.

Kützing, Tab. Phyc. Bd. xv. 1865, tab. 61, p. 22.

Chagos Archipelago, Diego Garcia; in alcohol.
Distribution. Indian Ocean.

The specimens come near to some forms of *L. obtusa*, but they are distinguished by their small size. I think that until all the forms of *L. obtusa* from the East Indies are better known, we may retain Kützing's species.

5. Laurencia pygmæa, n. sp. (Plate 12. fig. 6.)

Fronde tereti, filiformi, tenui, circa 1 cm. alta, pulvinatim cæspitosa, intricata; ramis primariis decumbentibus, secundariis erectiusculis; ramulis clavatis, truncatis. Ramis primariis usque ad 250 μ crassis, ramis secundariis et ramulis tetrasporiferis 100–150 μ crassis. Cystocarpiis et antheridiis non visis.

Chagos Archipelago, Diego Garcia, no indication of depth; in alcohol.

Laurencia pygmæa is distinguished by its size, which is indeed dwarf for a *Laurencia*. It grows in tufts, and the alcohol material looks as if it had grown on stones or shells and had been cut off with a knife. The thallus consists of decumbent branches—I have seen no rhizoids—which give off suberect ascending ones; these are branched irregularly. Sometimes the ramuli are subopposite, sometimes subverticillate or even single. They are always slender, and not particularly short as are the ramuli of *L. pannosa*, Zan. From this plant, *L. pygmæa* may also be known by its thalli, which, though intricate, are easily teased out under a pocket-lens, whereas in the case of *L. pannosa* this cannot be done, according to Zanardini, without damaging the frond. The mode of branching reminds me of *L. obtusa*, but the thallus is very slender, the main branches having a diameter of 200–250 μ and the side-branches and tetrasporiferous ramuli from 100–150 μ. Characteristic for this small alga are the swollen light-reflecting lateral membranes of the central cells. From *L. indica*, Hauck, it is easily known by its small size.

6. Laurencia ceylanica, J. Ag.

J. Agardh, Epicrisis Syst. 1876, p. 660.
De Toni, Syll. Alg. vol. iv. sect. iii. 1903, p. 805.

Amirante, at 20 fms.; dried specimen and in alcohol.
Coetivy, reef; in alcohol.
Distribution. Ceylon.

Subfam. Chondrieæ.

Acanthophora, Lamouroux.

1. Acanthophora orientalis, J. Ag.

J. Agardh, Species Algarum, ii. 1863, p. 820.
De Toni, Syll. Alg. vol. iv. sect. iii. 1903, p. 822.
Börgesen, "Some new or little-known West Indian Florideæ, ii.," in Bot. Tidsskr. Bd. xxx. 1910, p. 201.

Terné Mahé; dry specimen.
Seychelles, Long Island; dry specimen.
Distribution. Zanzibar; Malay Archipelago; North Australia; Tonga Archipelago; Marianne Islands.

Both specimens are full grown and large, but both are barren, and thus a study of the stichidia is out of the question. In a recent paper Mr. Börgesen has called attention to the fact that the name of *A. Thierii* ought to be changed to *A. spicifera* and that the antheridia of *A. orientalis* are very much like those of *A. spicifera*.

Pseudendosiphonia, n. g.

Thallus radicibus parvis substrato affixus et verisimiliter horizontaliter expansus, constat ex axi principali, ramis lateralibus incremento infinito et ramis dorsalibus ventralibusque incremento finito. Ad apicem vegetationis axis principalis radiatim se findit; axis principalis postea etiam inferius bilateralis. Axes laterales eodem modo quo axis principalis nascuntur. Thallus formatus e cellula centrali et quatuor cellulis pericentralibus pluribus stratis cellularum corticalium peripheriam versus diminutarum cinctis. Cystocarpia et antheridia ignota. Stichidia in apice pedicelli monosiphonii, sporam unam in singulis segmentis continentia. Pedicellus monosiphonius ramificatus; stichidia nuda.

1. Pseudendosiphonia Gardineri, n. sp. (Plate 13. figs. 13–15; Plate 14. fig. 30.)

Stichidiis sparsis extra axillaribus; ceteroque confer diagnosin generis.
Amirante, 20–25 fms.; in alcohol.

Pseudendosiphonia Gardineri recalls, by its short thorny branches and its stichidia borne on a monosiphonous stalk, the genus *Endosiphonia*. It has, however, a different

habit, having a well defined stem and regularly placed lateral branches, whereas *Endosiphonia* has no definite stem nor regular ramification. Anatomically the genus is characterized by its four big pericentral cells (fig. 30, *p.c.*), surrounded by several layers of cortical cells which are always much smaller. In *Endosiphonia* the four pericentral cells are surrounded by cells of the same size.

The stem of *Pseudendosiphonia* is attached to small flat stones or particles of rock by means of small rhizoids and around it stand four branches with a divergence of $\frac{1}{4}$; they take their origin from the central cell and are therefore endogenous; the lateral ones are of unlimited growth (Langtriebe), the dorsal and ventral ones remain short (Kurztriebe). The lateral branches have the same development as the principal stem, but their side-branches remain at first short and give the plant a thorny appearance that strongly reminds one of *Endosiphonia*. At the top of some branches there are luxuriously developed trichoblasts ("leaves," Falkenberg), but on most they had fallen off, probably because they have so many side-branches and such large cells.

The stichidia bear a great resemblance to those of *Endosiphonia*, particularly to *E. clavigera*, for they are placed irregularly on the stem and branches (Pl. 13. fig. 14) and not in the axils of the latter. They spring from peripheral cells and have a monosiphonous pedicel, but this bears branches, which is not the case with *E. clavigera*. The stichidium itself was bare in all the specimens examined, but I think it likely that the branches of the pedicel may develop further stichidia. I noted at the top of these branches some divided cells that I thought would develop into stichidia, but no later stages were observed. The cells covering the tetraspores in the stichidium are not horizontally disposed as in *Endosiphonia* but are arranged more or less obliquely. It is not certain, however, how far this may change as the sporangium attains maturity. This alga differs from the genus *Endosiphonia* by its habit and anatomical structure, and though nearly related to it, I believe I am justified, on account of these differences, in describing it as a new genus.

I have great pleasure in dedicating this interesting species to Mr. J. Stanley Gardiner.

Cladhymenia, Hooker et Harvey.

1. Cladhymenia oblongifolia, Hook. et Harv. (Plate 12. fig. 7.)

Hooker et Harvey, Alg. Nov. Zel. no. 70.
De Toni, Syll. Alg. vol. iv. sect. iii. 1903, p. 850.

Amirante, 25 fms.; dry specimens and in alcohol.

Distribution. New Zealand.

The specimens from Amirante are small (Pl. 12. fig. 7) but identical with some that I received from Prof. J. Agardh from New Zealand under the name of *Cladhymenia oblongifolia*, var. I think that the small size of the Amirante specimens may be accounted for by the great depth from which they come.

Chondria, C. Agardh.

1. Chondria pumila, Vick. (Plate 12. fig. 8.).

Vickers, "Liste des algues marines de la Barbade," in Ann. d. Sc. Nat. 9me série, Bot. vol. i. p. 45.

Chagos Archipelago, Diego Garcia, no indication of depth; in alcohol.

Distribution. Barbados.

On comparing the *Chondria* from the Chagos Archipelago with *Ch. pumila*, Vick. from Barbados, I could detect no character whereby to distinguish it. I conclude, therefore, that they belong to one species even though the distance between the two localities is very great; but perhaps this minute plant will be detected later in intervening localities. Miss Vickers intended to give a figure, but her untimely death prevented her from carrying out this intention. I have therefore given an illustration of the Chagos plant.

2. Chondria simpliciuscula, n. sp. (Plate 12. figs. 9, 10.)

Thallo filiformi, repente, intricato, pauci ramoso; ramis interdum oppositis, plerumque singulis; apice filorum truncato, cellulis apicalibus in fovea crateriformi immersis. Cellula centrali et quinque cellulis pericentralibus uno aut duobus stratis cellularum corticalium circumdatis. Cellulis periphericis desuper visis ad apicem hexagonalibus, in parte inferiore cum pariete undulata et ea re moniliformi. Organis fructificationis non visis.

Aldabra, reef, on *Laurencia papillosa*.

This small species is characterized by its filaments being mostly horizontally disposed, sparingly branched, and bearing the tetrasporangia not in special stichidia but at the apex of ordinary branches, which ultimately may grow out into long vegetative shoots when the formation of tetraspores has ceased.

After having been dried *Ch. simpliciuscula* adhered firmly to the alga on which it had spread itself, but I detected no union between the two plants. It belongs to the section *Cœlochondria*, Falk., as is clearly shown by fig. 10 on Pl. 12.

Polysiphonia, Greville.

1. Polysiphonia spec.

Praslin, reef, on *Hypnea pannosa*.

A fragmentary specimen that I was unable to name.

Roschera, Sonder.

1. Roschera glomerulata (Ag.), n. comb.

Tolypiocladia glomerulata, Schmitz, Marine Florid. von Deutsch Ost-Afrika, 1895, p. 160.

Seychelles, Long Island; dry specimen.

Distribution. Zanzibar; Indian Ocean; Malay Archipelago.

A small fragment, attached to *Gelidiopsis variabilis*. In the 'Siboga' paper I hope to point out that Schmitz was perfectly right, when he supposed that *Roschera africana*, Sonder, and *Tolypiocladia glomerulata* belonged to the same genus. I have therefore made use in this paper of Sonder's older generic name.

Herposiphonia, Naegeli.

1. Herposiphonia prorepens (Harv.), Schm.

Harvey, Phycol. Australica, tab. 185 (B).

Chagos Archipelago.

Distribution. Algoa Bay; Western Australia.

After describing the present plant, Harvey adds: "This alga was first described from Algoa Bay, where it occurs on corallines. The Australian plant is more slender, with fewer tubes, but otherwise the same." The *Herposiphonia* on *Dasyopsis Geppii* has 8 pericentral tubes; it stands therefore nearest to Harvey's Australian form. My material is too scanty to make out whether these forms are specifically distinct from the Algoa plant, as some authors have thought probable.

Oligocladus, Weber-van Bosse.

1. Oligocladus Prainii *, n. sp. (Plate 14. fig. 31.)

Thallo filiformi repente, ramis normaliter dorsaliter exeuntibus, erectis, endogenis, ramulos unilaterales ferentibus. Filo constante ex uno ordine cellularum centrali et ex quattuor ordinibus cellularum pericentralibus. Trichoblasti desunt. Filis latis 120–200 μ, ramulis 12–80 μ. Organis fructificationis ignotis. Rhizoidis unicellularibus.

Coetivy, reef, on *Dasyopsis aperta*; in alcohol.

The alga that I have named *Oligocladus Prainii* belongs to the subfamily of the Herposiphoneæ, and is very nearly allied to the new genus *Oligocladus*, provisionally described in 'Annales du Jardin Botanique de Buitenzorg,' 1910, p. 31. The specimens were found growing among the penicilli of *Dasyopsis aperta* and are barren; the determination is therefore not quite certain, but in anatomical structure these algæ so closely resemble *O. Boldinghii*, Web. v. B., that I feel almost sure that they belong to this genus. I may also add, that in a few long branches I have seen a condensation of protoplasm in two cells of each segment. This reminded me of the two sporangia in each segment in *Oligocladus Boldinghii*, but in the present case I could not detect the slightest trace of division in the protoplasm. They were, however, too young, and I must leave it to future investigators to settle the question.

O. Prainii is a creeping filamentous alga with four pericentral cells, dorsally placed, endogenous branches, and unicellular exogenous ventral rhizoids. Thus far it is like *O. Boldinghii*. It differs from this alga in having no trichoblasts, but a naked, straight

* Named in honour of Sir David Prain, in remembrance of a lovely walk in the Botanical Gardens at Calcutta.

apical cell, and a much denser ramification. The absence of trichoblasts is no reason to separate *O. Prainii* from the genus *Oligocladus*, for in the genus *Polysiphonia* we find species with and without these organs.

The main axis of the plant was attached by means of its long rhizoids to the branches of *Dasyopsis*, and, as may be seen in fig. 31, the youngest part raises itself from its support, grows vertically upwards, though its apex shows a slight curve. The apical cell is rather long and cuts off the segments at its base by a transverse wall. These segments remain undivided for a long time—I have counted eight of them under the apical cell before the pericentral cells are begun to be cut off.

The dorsally placed branches arise irregularly with a distance of 3, 4, 6, 7, 8, 9, and even more segments between them; they bear branches of the second order on the side turned towards the main axis. In some cases I observed near the apex of the main axis long ramified branches alternating with short simple ones, but in later stages I could detect no further difference. Perhaps the long ones bear the tetrasporangia and the short ones remain sterile, but this is a mere suggestion. The first segment of the branches issuing from the main axis has only short pericentral cells; the second segment has pericentral cells of the normal size; all the branches of the first and second orders arise from the central tube. The size of the branches and of the main axis differs considerably according to the place where the measurement is taken. The main axis has a breadth of 120–200 μ; the branches 40–80 μ in the lower parts, but at the top only 12–20 μ; the segments are $1\frac{1}{2}$ times as long as the diameter, and at the top as long as broad.

At the top of the main axis all the branches are arranged on the dorsal side of the filament, but at some distance from the apex their position is sometimes altered; this is the result of a slight twisting of the cells of the main axis.

2. Oligocladus pusillus, n. sp.

Thallo filiformi, repente; ramis erectis, endogenis, simplicibus, normaliter dorsaliter exeuntibus. Filis constantibus ex uno ordine cellularum centrali et quattuor ordinibus cellularum pericentralibus. Trichoblastis numerosis, filorum apices cingentibus. Filis latis 40–100 μ. Organis fructificationis ignotis. Rhizoidis unicellularibus.

Coetivy, reef, on *Dasyopsis aperta*; in alcohol.

Oligocladus pusillus, on account of the numerous trichoblasts that surround the slightly curved top, stands nearer to *O. Boldinghii* than *O. Prainii*. It is a smaller plant, though its filaments are broader. Its creeping filaments give off side-branches on the dorsal side at a distance of 5, 7, 12, 20 segments and even more. These ascending side-branches remain simple; when, however, they develop into creeping filaments, as occasionally happens, they likewise give off branches on their dorsal side. The creeping branches have a diameter of 100 μ, the side-branches a little less, and at the top of both the diameter sinks to 40 μ. The segments have a height of 80–100 μ, but this sinks at the top to 20 μ and even less.

Organs of fructification have not been observed.

Dasyopsis, Zanardini.

1. Dasyopsis Stanleyi, n. sp. (Plate 13. fig. 16.)

Thallo elongato, subdichotomo, pauce ramoso, penicillis longis, gracilibus cincto; ramificatione radiata, constante e penicillis basim versus deciduis, spinas non relinquentibus. Stichidiis oblongis et cystocarpiis ex penicillis orientibus. Antheridiis non visis. Thallo alto 16 cm. Habitu *Dasyæ elegantis*.

Cargados Carajos, 30 fms.; in alcohol and dry specimens.

To rightly understand the new species of *Dasyopsis*, it may be worth while to give a short account of the characters of the genus. *Dasyopsis* has a sympodial mode of growth; the stem or axis being composed of short branches with definite growth; these are pushed aside by their own first branch, and the distance between the base of the mother-branch and the point of insertion of its first branch varies in different species.

But this is a feature *Dasyopsis* has in common with all Dasyeæ; its special character consists in the absence of true pericentral cells. The cells that surround the central tube are not originally segments of this tube, as in the other Rhodomelaceæ, but they are downward-growing hyphæ, the mother-cell of which is cut off from the branch that is pushed aside when sympodial growth sets in (Pl. 14. fig. 32, *m*). The hyphæ may be of the same diameter as the central cells, in which case they resemble true pericentral cells, but they have quite a different origin. The displaced branches continue to develop, they are shorter or longer, naked or corticated, according to the species, and carry several monosiphonous filaments, the so-called penicillus, at the apex.

Dasyopsis Stanleyi consists of a subdichotomously divided principal axis or stem, carrying at indefinite intervals branches of unlimited growth, which may ramify again and are surrounded at the top by monosiphonous penicilli. This pretty alga so much resembles *Dasya elegans* that I felt at first inclined to take it for that species; after careful examination, however, I discovered that the plant has the characteristic structure of *Dasyopsis*; the branches of definite growth are separated by only one short segment from each other, and grow out in any direction from the main axis. As every branch or so-called penicillus gives off a downward-growing hypha, the central axis soon increases in thickness; true pericentral cells are of course absent.

The penicilli are composed of cells having a breadth of 6–13 μ; their length varies from being almost square at the base to 72 μ at the top. They are very delicate and soon fall off, unless they happen to bear cystocarps or stichidia at their base. The stichidia were very rare in my preparations; I observed only one but unfortunately lost it; I saw, however, that it was long and cuspidate. The cystocarps were numerous in fertile specimens.

2. Dasyopsis aperta, n. sp. (Plate 13. fig. 17; Plate 14. fig. 32.)

Thallo ex axibus principalibus primo surgentibus, postea decumbentibus constante, unde denuo rami adscendentes nascuntur. Apice axis principalis et ramorum penicillis ramulosis, monosiphoniis cincto, penicillorum pilis postea decidentibus, basi

monosiphonio brevi tantummodo restante. Thallo sympodiali, radiato; ramis cum divergentia $\frac{1}{4}$. Primo segmento libero ramorum ad basim satis magnam cellulam incremento basipetali disjungente. Cellulis centralibus magnis, hyphis numerosis angustis cinctis. Stichidiis ramulis penicillorum sessilibus; 8–10 sporas in unoquoque segmento ferentibus. Cystocarpiis et antheridiis ignotis.

Coetivy, reef; in alcohol.

This new *Dasyopsis* attains a height of 2·5 cm., and consists of a small tuft of primary ascending cylindrical axes or stems, that finally become horizontal and give rise to new ascending ones. The tufts, on growing older, become more or less intricate, but I never saw the fronds anastomose. *Dasyopsis aperta* is a good species for the study of the peculiar *Dasyopsis* structure, because the cells are large, even at the apex of the shoot. It is sufficient to spread the alga on the slide and to tear off carefully with a needle the surrounding penicilli to see plainly the row of central cells, each carrying a pushed aside apex and its first branch whose lowest cell builds up the sympodium. These branches stand spirally around the main axis, as far as I could ascertain, with a divergence of $\frac{1}{4}$, and carry long, incurved filaments at their top, which form together the penicillus. The first cell, after the branch has been pushed aside, cuts off a cell at its base (Pl. 14. fig. 32, *m*); this is the mother-cell of the downward growing hyphæ, which are at first almost as large as the cells of the central axis or tube. At the top of a stem or axis, where the mutual position of the different cells is still unaltered, the central tube appears to consist of a central and four pericentral cells, but on following the pseudo-pericentral cells to their origin, it will be clearly seen that they are downward growing hyphæ, arising from the first free cell of the pushed aside branch. The sympodial axis is afterwards covered by a thick layer of smaller hyphæ, which by growing between them alter the original position of the cells.

The stem or main axis is cylindrical, though tapering towards its apex, which is densely covered with penicilli; these, however, soon fall off, and the base of older stems is almost denuded, though not entirely, for remnants of the basal portion of the penicilli often remain.

The sessile stichidia are borne on the side-branches of the penicilli; they are cylindrical and, when the tetrasporangia have acquired their full size, a little torulose. I counted from 6–8 sporangia in different segments; and the whole is crowned by one or two barren cells. Neither cystocarps nor antheridia were seen.

There are, according to Falkenberg*, two other species of *Dasyopsis*, which, like *D. Stanleyi* and *D. aperta*, have penicilli facing every way, namely *Dasyopsis spinella* and *D. cervicornis*. From the first both *D. Stanleyi* and *D. aperta* differ in the absence of the little spines that have given *D. spinella* its specific name, and from *D. cervicornis* in the shape of their stem, cylindrical throughout, not angular at the insertion-point of the penicilli.

* Falkenberg, 'Die Rhodomelaceen des Golfes von Neapel,' 1901, p. 667.

3. Dasyopsis Geppii, n. sp. (Plate 13. figs. 18-20; Plate 14. fig. 33.)

Thallo carnoso, plano, palmato, inciso, horizontaliter expanso, sympodialiter constructo, ad apicem radioso; divergentia ignota. Penicillis lateralibus tantum bene evolutis, dorsalibus et ventralibus aliquamdiu conspicuis, postea evanescentibus. Ramis lateralibus pro parte cum axi principali coalitis. Strato corticali cellularum rotundarum aut angulosarum contiguarum. Antheridiis cylindricis in turmis in facie inferiori thalli sitis. Cystocarpiis et stichidiis ignotis.

Amirante, 20–25 fms.; in alcohol.

Cargados Carajos, 25 fms.

Chagos Archipelago, Solomon Island, no indication of depth; in alcohol.

Coetivy, reef.

Dasyopsis Geppii has a broad, flat, fleshy frond, slightly palmatifid and attached to the substratum by a thick pedicel (Pl. 13. figs. 18, 19). Its outward appearance differs entirely from any known species of *Dasyopsis*, and it is only by the study of the youngest segments of the frond that an insight into its anatomical structure is obtained. This is in principle like that of *Dasyopsis*, but differs in so far as the displaced branches, instead of turning in every direction, as they do in *D. Stanleyi*, spread themselves principally in a bilateral direction and grow congenitally into a leaf-like frond. The penicilli are situated on the margin of this frond, but also on its upper and lower surface; the cells of the filaments have a breadth of 16–28 μ, and a length of 32-88, 100, and 140 μ.

At the top of the different segments the penicilli are so closely packed together, in consequence of the smallness of the cells, that it is impossible to trace the central tube down into the frond or to observe the divergence of the penicilli around its apex (Pl. 14. fig. 33).

Dorsi-ventral organization does exist, though I could not trace it at the apex of the frond. The ventral side, that turned towards the substratum, bears antheridia at the base of old penicilli. The antheridia stand in groups of five and six together (Pl. 13. figs. 19, 20), and are borne on a monosiphonous pedicel. The dorsal side of the frond is barren in all my specimens. The position of the antheridia is interesting, for *D. Geppii* is both a reef and a deep-water plant. If it were only collected on the reef, one might infer that the antheridia kept to the ventral side to ensure protection from the sun, but since these algæ have been found with ventrally placed antheridia, not only on the reef but also in deep water, this explanation does not hold good. Dorsi-ventral organization of any kind was hitherto unknown in *Dasyopsis*.

I have great pleasure in dedicating this alga to my kind friend, Mr. Gepp, of the British Museum.

4. Dasyopsis palmatifida, n. sp. (Plate 13. fig. 21.)

Thallo carnoso, plano, profunde palmatifido, segmentis aut laciniis sæpe terminantibus in filamento cylindrico, substrato bulbo affixo. Segmentis ad apicem radiatis, postea horizontaliter expansis. Penicillis circum apicem thalli bene evolutis, infimis evanescentibus. Penicillis constantibus e filis multo crassioribus quam

penicillis *Dasyopsis Geppii*; filis stichidia in apicibus pedicellorum brevium monosiphoniorum circumdantibus. Stichidiis sporis numerosis. Cystocarpiis et antheridiis ignotis.

Amirante, 20–25 fms.; in alcohol.

Chagos Archipelago, Solomon Island; in alcohol.

Coetivy, reef; in alcohol.

Dasyopsis palmatifida resembles in essential points *D. Geppii*, but its frond is far more deeply palmatifid and the different segments often terminate in a cylindrical branch. These fasten themselves to any hard object and produce at that spot a little tubercle, which much resembles the thick pedicel of *D. Geppii*. I have considered the question whether *D. palmatifida* might not be the stichidia-bearing form of *D. Geppii*, but have been unable to solve it. In addition to its deeply palmatifid frond, *D. palmatifida* differs also from *D. Geppii* in the size of the filaments forming the penicilli; these cells having a length of 104–106 μ and a breadth of 12-20, 36-40 μ. Stichidia with tetrasporangia are borne at the base of the penicilli on monosiphonous pedicels; they have a blunt apex.

Tapeinodasya, Weber-van Bosse.

1. Tapeinodasya Ethelæ, n. sp. (Plate 13. figs. 22, 23.)

Thallo procumbente, constante e sympodio bilaterali; tertio quoque segmento aut ramulum lateralem spinosum incremento finito ferente, aut ramulum lateralem spinosum incremento sympodiali infinito. Ramulis adventitiis præterea ex axillis ramulorum spinosorum emergentibus sed parvis etiam adultis. Axi constante e cellula centrali cum quattuor cellulis pericentralibus; quo numero verumtamen cellularum pericentralium in segmentis sæpe majore ob concrescentiam ramulorum. Axi centrali cellulis corticalibus, peripheriam versus diminutis, cincto. Hyphis numerosis in parietibus inter cellulas pericentrales nascentibus. Organis fructificationis ignotis.

Amirante, 20–25 fms.; dry and in alcohol.

Tapeinodasya Ethelæ is the second known species of this genus; the type, *T. Bornetii*, being described in the 'Recueil des Travaux botaniques Néerlandais,' No. 1, 1904. The plant from Amirante differs in having a less dense ramification, which is, as a rule, bilateral. The branches have the outward appearance of little spines. At the top of the main axis they point outwards in three directions, but immediately below the growing-point the branches stand in two rows. In my preparations the distance between the succeeding branches in the sympodium is three cells, but I should not be surprised if in parts of the frond the distance amounted to only two cells, as in the other species, *T. Bornetii*, the number is known to vary. The branch that is displaced ends in a spine; it is either of definite growth and develops no further, or of indefinite growth, in which case it may give rise to a lateral sympodial branch. The branches grow congenitally with the main axis for one or two segments, and in a cross-section through such a segment a greater number of pericentral cells is visible.

The central cell is surrounded normally by four pericentral cells, but between these other large cells soon appear and numerous hyphæ develop in the membranes. I have not seen them enter the pericentral cells as they do in *T. Bornetii*, but it may be that this takes place in the basal part of the frond. A layer of small cortical cells surrounds the main axis. The latter has a winged appearance on account of the pericentral cells of the spine-like lateral branches growing sideways together with it for a few segments.

Adventitious branches appear occasionally on the dorsal side of the frond in the axil of lateral branches, but they remain short; in *T. Bornetii* these branches attain full development.

The characteristic dorsi-ventral organization of *T. Bornetii* is far less conspicuous in *T. Ethelæ*, and shows itself in barren specimens only in the rudimentary axillary branches. No organs of fructification were present, and it was only because I was familiar with the genus that I was able to name the specimens from Amirante.

Heterosiphonia, Montagne.

1. Heterosiphonia Rendlei, n. sp. (Plate 12. figs. 11, 12.)

Thallo fasciculato, pluribus ramis principalibus e callo basali surgentibus; ramis principalibus totis ecorticatis, pauce ramosis, penicillos ad segmentum quodque secundum, distichos et alternantes gerentibus. Cellulis pericentralibus 7–8–10. Penicillis ramulos unilaterales et stichidia potius obtusa quam acuta ferentibus tetrasporis instructis. Antheridiis et cystocarpiis ignotis. Thallo alto 8 cm.

Cargados Carajos, 47 fms.; dry specimen.

I believe *Heterosiphonia Rendlei* * to be a new species because none exists amongst the *Heterosiphoniæ ecorticatæ* that is exactly like it. It belongs to the small group with more than four pericentral cells, the branches or penicilli of which arise at a distance of two or three segments from each other and are turned regularly to the right and left. *H. Rendlei* stands nearest to *H. subsecundata* (Suhr), Falk., but differs in the pericentral cells not being transversely divided.

The principal axis has a height of about 8 cm.; it is erect and carries small horizontally spread penicilli which have unilateral monosiphonous branchlets incurved at the top. The number of pericentral cells in the main axis varies from 6–10, and the segments are three times as broad as long. In the penicilli the few basal polysiphonous segments are almost as long as broad or a little broader.

I have seen neither cystocarps nor antheridia, only stichidia, which are borne on the side-branches of the penicilli; they are elongated with a blunt apex.

2. Heterosiphonia spec.

Coetivy, reef; dry specimen.

This is a small specimen, 1 cm. high; it grows on *Codium*. I failed to recognize it amongst the described species and yet do not dare to describe it as new.

* Named in honour of Dr. Rendle, Keeper of the Botanical Department of the British Museum, renowned for the kind hospitality that it offers to every visitor.

Amphisbetema, n. g.

Thallus constat e pede crasso rhizomatoideo, unde nascuntur axes erecti, corticati, regulariter sympodii modo compositi e ramis incremento finito conspicue monopodialibus dorso-ventraliter crescentibus. Axis constat ex una cellula centrali et sex cellulis pericentralibus, tribus aut quatuor ordinibus cellularum longitudine cellulæ primariæ pericentralium cinctis; quos ordines stratum corticale crassum e cellulis parenchymaticis fissis compositum cingit. Cystocarpia et antheridia ignota. Stichidia sporis verticillatis, æque ac in *Dasya* non omnino cellulis corticalibus obtectis.

1. Amphisbetema indica (J. Ag.). (Plate 13. fig. 24; Plate 14. fig. 34, and text-fig.)

Dasya indica, J. Agardh, Till Alg. Syst. xi. 1890, p. 111.

Diagnosis the same as that of genus.

Aldabra, reef, Passi Honakan, outside; dry specimens.

Distribution. Diego Garcia.

The alga for which I propose the generic name of *Amphisbetema* was described in 1890 by J. Agardh under the name of *Dasya indica*; the structure of the stichidia, almost identical with that of *Dasya*, probably induced this eminent algologist to describe the plant under that name, for he was quite cognisant of the differences in ramification between his alga and other *Dasyæ*. In De Toni's 'Sylloge Algarum,' iv. p. 1146, 1903, *Dasya indica* has received the name of *Wilsonæa* (?) *indica*.

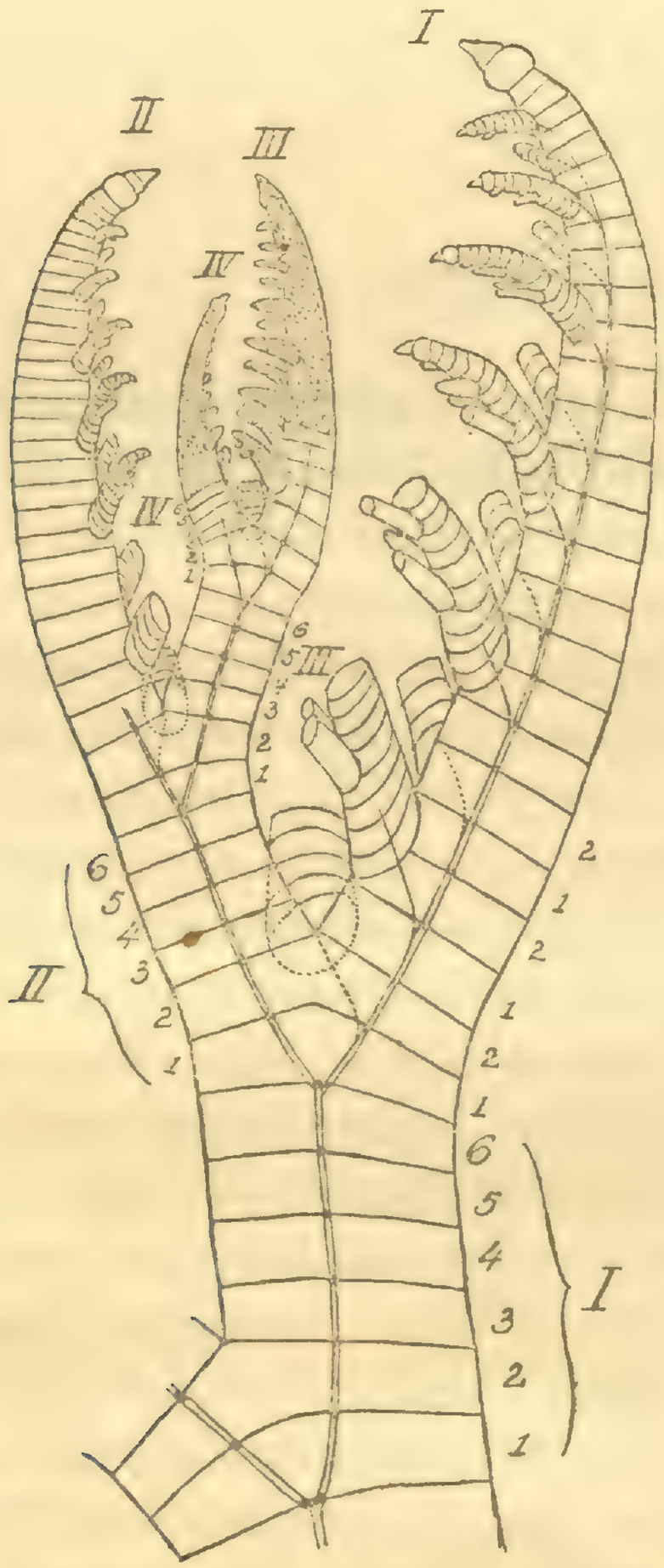
I found this alga in the collection of Mr. Stanley Gardiner, and through the kindness of Sir David Prain I was able to compare it with authentic material from Diego Garcia, now preserved in the Herbarium at Kew, and I wish to express my best thanks to him for so liberally placing this material at my disposal. The study of the type-specimens enabled me to identify my barren material from Aldabra. This differs only from the type in being a little stronger; the algæ from Diego Garcia bear stichidia with tetrasporangia, a fact which may account for their being more slender.

Amphisbetema has a strong rhizome-like base from which arise erect main axes, attaining a height of 8–9 cm., with distichous bilateral branches. These main axes are composed of branches or shoots of definite growth, succeeding each other at a distance of six segments to be then displaced by their own first branch. The branches have, as far as I could make out, monopodial growth; sympodial growth sets in only when each in turn is pushed aside. All the branches have a dorsi-ventral organization; their first branch of the second order is always inserted at a distance of six segments from the base, and all the succeeding ones at a distance of two segments; they stand in two rows on the ventral side of the branch, and only by subsequent growth do they ultimately take their bilateral position. The branches of the second order have the same ramification as the primary ones and are always turned to one side; each principal branch carries as a rule six pairs of branches of the second order; but the nearer to the apex the less do they develop.

After the formation of these six pairs of branches, the vigour of each mother-branch seems to be exhausted. At a distance of three or four cells from the apex,

a segment remains undivided: its contents, balled together, look like a large drop of oil and have a reddish-brown colour. The first segment succeeding this undivided cell may show a division into a central and pericentral cells, the next is undivided, and the ultimate one has usually the shape of a spine. Sometimes the top of a branch is crowned by a simple or ramified monosiphonous filament. I could find no explanation for this difference in development; the monosiphonous filaments are not trichoblasts, nor could any trace of these organs be detected. The large undivided cell, with the cells above it, fall off after a shorter or longer period, and the branch that carried them is blunt in consequence.

Fig. 1.



Schematic figure of apex of *Amphisbetema indica*, showing the sympodial growth of main axis and the monopodial growth of the displaced shoots. After 6 segments shoot I is pushed aside by its first branch, shoot II is also displaced after 6 segments by its first branch, and the other shoots follow in like manner. The displaced shoots carry side-branches at every second segment.

The axes have in each segment a central and six pericentral cells; in the last-formed side-branches this number may sink to four, but as a rule it is six. The pericentral cells, in common with those of *Endosiphonia* and *Melanothamnus*, cut off to the outside cells quite as long as themselves; and this may be repeated several times. In the branches the cells on the dorsal side are a little longer than those on the ventral, but this difference disappears with subsequent growth. The whole central strand is surrounded by a rather thick layer of parenchymatous cells. The peripheral cells are of equal size and elongated longitudinally, not radially as in *Melanothamnus*. Though the cortical layer is pretty

thick, the transverse membranes of the succeeding segments within are plainly visible, owing to the fact that the central strand consists of a large number of cells of equal length. The segments are short, and this fact gives, whenever the apex of a shoot is pushed aside, the impression that the main axis is divided into three branches. Careful examination will, however, show that this impression is erroneous, being brought about by the displaced shoot, its first branch—the new shoot—and its second branch standing very close together, owing to the short segments and the congenital growth of the first two segments.

My plants are barren: J. Agardh, however, described the stichidia, which he stated were like those of *Dasya* and bore verticillately developed tetraspores partially uncovered on the outside.

Amphisbetema has received its name * on account of the difficulty experienced in assigning to it its true systematic position. It has characters in common with several genera of Rhodomelaceæ and also with *Melanothamnus*, Born. et Falk., a genus of uncertain position so long as the organs of fructification remain unknown.

With *Strebloclad*ia, *Amphisbetema* agrees in the regular alternating mode of monopodial and sympodial growth; with *Melanothamnus* and *Endosiphonia* in the numerous secondary pericentral cells of equal length; with *Heterosiphonia* in the dorsi-ventral organization of its branches; and with *Dasya* in the structure of the stichidia.

The association of all these characters in one genus makes me inclined to consider *Amphisbetema* as an old form of Rhodomelaceæ which existed before the genera that have now developed one or more of the characters—in our new genus still blended together—in their own special way and to the exclusion of the other characters.

Dictyurus, Bory.

1. Dictyurus purpurascens, Bory.

Bory de St. Vincent, in Bélanger, Voy. Indes orient. p. 170.
Falkenberg, Die Rhodomelaceen, 1901, p. 675.
De Toni, Syll. Alg. vol. iv. sect. iii. 1903, p. 1173.

Saya de Malha, 55 fms.; dry specimen.
Coetivy, reef; dry specimen and in alcohol (fragment).
Cargados Carajos, 30 and 47 fms.; dry specimen and in alcohol.
Amirante, 30 fms.; in alcohol.
Chagos Archipelago, Solomon Isl., 22 fms.; in alcohol.
Distribution. Cape Comorin; Coast of India; Mauritius; Ceylon; Malay Archipelago.

Fam. CERAMIACEÆ.

Griffithsia, C. Agardh.

1. Griffithsia spec.

Amirante, 20–25 fms.; in alcohol.
Only a small fragment, but with the characteristic tetraspores of the genus.

* ἀμφισβήτημα, controversy, a point in dispute.

Haloplegma, Montagne.

1. Haloplegma Preissii, Sond.

Sonder, Alg. Preiss, p. 24.
Harvey, Phyc. Austr. 1859, tab. 79.
De Toni, Syll. Alg. vol. iv. sect. iii. 1903, p. 1366.

Cargados Carajos, at 22, 30, and 47 fms.; both dry and in alcohol.

Distribution. Western Australia; Tasmania, in the River Tamar above Georgetown; Malay Archipelago.

The specimens of *H. Preissii* from Cargados Carajos are shorter, less branched, and more flabellate than most plants found in the herbaria under that name. I have not ventured, however, to describe these specimens as new, for I have found no microscopic character to distinguish them from the type, the size of the main branches and the peripheral filaments being essentially the same in the different plants. The specimens from Cargados Carajos bear tetraspores; I have not seen cystocarps or antheridia, and it is possible that these may show differences in structure. Dr. Harvey, in his 'Phyc. Australica,' however, calls attention to the fact that the external form of *H. Preissii* is very variable. He found it growing in the River Tamar, a considerable distance above Georgetown, where it appeared at first to be a distinct species; but he was able to trace it down to the Heads of Port Dalrymple, and found that it blended into the usual variety. I feel very much inclined to think that the specimens from Cargados Carajos owe their small size in great measure to the depth at which they were gathered.

Antithamnion, Naegeli.

1. Antithamnion adnatum, J. Ag.

J. Agardh, Analecta algologica, 1892, p. 12.

Solomon Island.

Distribution. New Zealand; Malay Archipelago.

A small specimen with tetraspores, attached to *Herposiphonia*.

Spyridia, Harvey.

1. Spyridia filamentosa (Wulfen), Harv.

Harvey in Hooker, Brit. Flora, vol. ii. p. 337; Phycol. Brit. 1871, pl. xlvi.

Aldabra reef, outside Passi Honakan.

Distribution. West Indies; Mediterranean; Red Sea; Indian Ocean; Malay Archipelago.

Only a small fragment attached to *Amphisbetema indica*.

Ceramium (Roth), Lyngbye.

1. Ceramium cinnabarinum (Gratel.), Hauck.

Hauck, Die Meeresalgen von Deutschland, 1885, p. 112.

Solomon Island.

Distribution. Mediterranean; Malay Archipelago.

A small specimen amongst other Algæ.

2. CERAMIUM spec.

Cargados Carajos, 47 fms.
On *Heterosiphonia Rendlei*; barren specimens.

REINBOLDIELLA, De Toni.

1. REINBOLDIELLA SCHMITZIANA (Reinb.), De Toni.

Phyceæ japon. novæ, 1895, p. 35.
Gloiothamnion Schmitzianum, Reinbold, in Hedwigia, 1895, p. 205.

Chagos Archipelago, Egmont Reef; in alcohol. On *Gelidiopsis*.
Solomon Island. On *Gelidium*.
Distribution. Japan; Malay Archipelago.

Fam. GRATELOUPIACEÆ.

HALYMENIA (C. Ag.), J. Agardh.

1. HALYMENIA POLYCLADA, A. & E. S. Gepp.

Var. ALDABRADENSIS, n. var.—Thallo e callo basali subito cuneatim expanso 10 cm. alto, 4–5 cm. lato deinde palmati-partito constante; ramis usque ad 6 cm. longis, 0·5–1 cm. latis, ramulis lateralibus iterum iterumque subdichotomicis pinnatis, angustis.

Aldabra, outer reef; dry specimens.
Distribution. Christmas Island.

Halymenia polyclada belongs to Agardh's *Acanthymenia* section of *Halymenia*. According to Schmitz, it is highly probable that this group is identical with the genus *Gelinaria*, Sond. Schmitz is further of opinion that the differences existing in anatomical structure are sufficient to separate *Acanthymenia* from the genus *Halymenia*. So long, however, as we do not know the cystocarps of the genus *Gelinaria* I think it more expedient to follow Agardh, although ultimately we will probably have to follow Schmitz and call the species of the *Acanthymenia* group by the generic name of *Gelinaria*.

The specimens from Aldabra are very similar to *H. polyclada*, which is nearly allied to *H. formosa*. It has a subdichotomous ramification, but lateral ramuli are plentiful along the margins of the upper branches. In the lower part of the fronds the margins are almost entire. It is a stronger plant than *H. polyclada*, but has the same short stalk expanding suddenly into a broad frond. In how far *H. formosa*, *Durvillæi*, and *polyclada* are really good species, is a question that future investigations must decide.

Cryptonemia, J. Ag.

1. Cryptonemia seminervis (Ag.), J. Ag.

J. Agardh, Algæ Liebman. p. 11 in not.
De Toni, Syll. Alg. vol. iv. sect. iv. 1905, p. 1610.

Saya de Malha, 55 fms.; dry specimens.
Amirante; dry specimen.
Distribution. Mediterranean; Atlantic; Red Sea.

In a dry condition the plants appear to have no midrib, but on moistening a delicate midrib became distinctly visible, and this extended upwards to about the middle of the leaf. The plants are barren.

2. Cryptonemia spec.

Saya de Malha, 55 fms.; dry specimen.

A poor fragment, but differing from *Cryptonemia seminervis* by its much thicker frond and dark red colour.

Fam. SQUAMARIACEÆ.

It is much to be regretted that so many of the specimens of Squamariaceæ collected by Mr. J. Stanley Gardiner are sterile, for without fruit it is almost impossible to name the genera and species of this puzzling family. I happened to have studied a large collection of Indian *Peyssonneliæ* before I undertook to name the present collection, and this has helped me to recognize some of the species mentioned hereafter.

In my "List of the 'Siboga' Algæ" I will treat in detail of the *Peyssonneliæ*, and only mention here that I have found it of great help to keep up a distinction already hinted at by the late lamented Schmitz*, namely, a distinction based on the differences in arrangement of the filaments of the hypothallus. These horizontal filaments, which run over the substratum, give off the ascending vertical filaments of the perithallus, and Schmitz observed that some hypothalli consisted of straight filaments running close to one another (*Peyssonnelia*), and that others consisted of curved fan-shaped groups of filaments, as in the basal layer of *Cruoriella*. To these two subgenera, if I may distinguish them provisionally by such a name, I wish to add a third, differing in having no hypothallus proper, but a mesothallus, *i. e.*, a layer of cells occupying the middle of the thallus (as is the case, for instance, in *Ralfsia expansa*), which gives off branches both downward and upward. My investigations do not yet allow me to decide whether this division of the genus *Peyssonnelia*, based as it is upon anatomical characters, is supported by differences in the structure of the fruit. Sometimes this is the case, but my specimens are mostly barren.

For this third subgenus I should like to propose the name of *Ethelia*, in honour of my dear friend, Mrs. E. S. Gepp.

* Schmitz, "Marine Florideen von Deutsch Ost-Afrika," in Engler's Bot. Jahrbuch, Bd. xxi. Heft 1, 2, 1895, p. 173.

Peyssonnelia, Decaisne.

Subgen. Eupeyssonnelia, n. subg.

Hypothallus filis arcte iunctis, flabelli modo fusis, maxime erectis.

1. Peyssonnelia coccinea, J. Ag.

J. Agardh, Epicrisis Floridearum, 1896, p. 385.
De Toni, Syll. Alg. vol. iv. sect. iv. 1905, p. 1695.

Seychelles, 31 fms.; dry specimen.

Distribution. West coast of Australia; Malay Archipelago.

The specimen is small and sterile; it was only by comparing it with 'Siboga' material that I was able to name it.

2. Peyssonnelia Harveyana (?), Crouan. (Plate 14. fig. 35.)

Crouan in J. Agardh, Spec. Algarum, ii. 1852, p. 501.
De Toni, Syll. Alg. vol. iv. sect. iv. 1905, p. 1694.

Saya de Malha, 55 fms., on several dry, calcareous, little pebbles.

Distribution. Coast of France, near Brest.

The specimens are of a bright red colour and adhere firmly to the substratum; they approach both *P. conchicola* and *P. Harveyana*, but on account of the large cells of the hypothallus I feel inclined to regard it as *P. Harveyana*. With regard to distribution, it is more likely that they belong to *P. conchicola*, an inhabitant of the Red Sea.

The specimens are all barren, and it is impossible to name them with certainty.

3. Peyssonnelia calcea, Heydr.

Heydrich, "Neue Kalkalgen von Deutsch Neu-Guinea" in Biblioth. Bot. von Frank u. Luerssen, 1897, p. 10.

Egmont, reef; in alcohol.

Coin Peros; in alcohol.

Distribution. Tami, near German New Guinea; Malay Archipelago.

The specimens bear nemathecia with tetraspores.

4. Peyssonnelia polymorpha (Zan.), Schmitz.

Form Gardineri, n. f.—Thallo primo adhærente, deinde a substrato soluto, tubera forma diversa, sed superficie lævi formante, colore parum rubro cum siccatus est. Hypothallo cellulis longis 36–44–60 μ, latis 8–10–16 μ. Perithallo constante e seriebus cellularum sursum directarum, cellulis infimis majoribus, cellulis superioribus minoribus, longioribus aut brevioribus quam latis; latis 16–20–24 μ. Organis fructificationis ignotis.

Amirante, 30, 45–60 fms.; dry specimens.

The specimens from Amirante are nearly allied to *P. polymorpha*, but the loose thalli are smaller and the crusts are thinner than in the typical specimens of that species. The anatomical structure of the two algæ is much alike, as far as the vegetative thallus is

concerned, and reproductive organs were not to be found. The cells of the f. *Gardineri* are perhaps, on the whole, somewhat smaller than those of the type, and seen from above f. *Gardineri* is covered by a smooth peripheral layer, which *P. polymorpha* had lost in all the specimens I have seen.

I conclude that f. *Gardineri* is a deep-water form of *P. polymorpha*.

Subgen. Ethelia, n. subg.

Mesothallus filis rectis aut ramosis, sinuatis, utroque latere fila perithalli emittens.

5. Peyssonnelia biradiata, n. sp.

Thallo per substratum extento, tantum hic illic adhærente, coriaceo, rubro, rotundo, diametro 2 ad 3 centimetrum, constante e mesothallo et perithallo. Mesothallo constante e filis ramosis, sinuatis, parva flabella efficientibus. Perithallo constante e filis sursum et deorsum directis. Perithallo summo diviso in partem inferiorem obliquam, cellulis magnis, et in partem superiorem erectam, hic illic zonatam, cellulis parvis. Organis fructificationis ignotis.

Seychelles, 31 fms.; dry specimen.

Distribution. Malay Archipelago.

A small but characteristic specimen.

Among the algæ from Saya de Malha there are several specimens that I believe belong to the genus *Peyssonnelia*, but they are unfortunately barren. They have much in common with the *Peyssonneliæ* of the *Ethelia*-group, for they have a mesothallus that gives off branches both in a downward and upward direction (Pl. 14. fig. 36). They are furthermore much calcified, hard as stone, and attached to bits of coral.

But besides these features found among the *Ethelia*-group, the *Peyssonneliæ* from Saya de Malha are characterized by long filaments (Pl. 14. fig. 37) almost free from each other and covered by a layer of pectic substance, which colours red with ruthenium. The filaments are like those we find in the sori of other *Peyssonneliæ*, but in the new plants they are not confined to sori alone, but cover the whole upper surface. Although I made sections through all parts of the thallus, I could find no trace of fructification.

We know that the fronds of *Stragularia* species amongst the Ralfsiaceæ are covered by filaments, and it appears probable that we have here something analogous amongst the *Peyssonneliæ*; but until the reproductive organs are discovered it is difficult to speculate as to these structures. A doubt still lurks in my mind whether, after all, these filaments may not belong to an encrusting parasitic alga; but it is well worth while to call attention to these specimens.

Cruoriopsis, Dufour.

1. Cruoriopsis cruciata, Dufour.

Dufour, Elenc. Alg. Lig. p. 35, after De Toni.
De Toni, Syll. Alg. vol. iv. sect. iv. 1905, p. 1689.

Saya de Malha; dry specimen on *Udotea*.

Distribution. Adriatic; Malay Archipelago.

The alga is barren, but its resemblance to specimens from Nias, Sumatra, bearing cystocarps and antheridia, is so great that I believe they belong to the same species.

Fam. CORALLINACEÆ.

Melobesia, Lamouroux.

1. Melobesia callithamnioides, Falk.

Falkenberg, Die Meeresalg. d. Golfes v. Neapel, 1878, p. 265.

Egmont Reef, on different algæ; in alcohol.

Distribution. Atlantic, Brest?; Mediterranean.

Amphiroa, Lamouroux.

1. Amphiroa fragilissima (Linn.), Lamx.

Lamouroux, Pol. flexibles, p. 300.

A. Weber-van Bosse and M. Foslie, "The Corallinaceæ of the 'Siboga' Exped.," Monogr. lxi. 1904, p. 89.

Chagos Archipelago, Solomon Island; in alcohol.

Distribution. West Indies; Pacific; Malay Archipelago; Dar-es-Salaam.

2. Amphiroa foliacea, Lamx.

Lamouroux, Voyage de l'Uranie par Freycinet, Zoologie par Quoy et Gaimard, p. 628.

A. Weber-van Bosse and M. Foslie, "The Corallinaceæ of the 'Siboga' Exped.," Monogr. lxi. 1904, p. 92.

Praslin; in alcohol.

Distribution. Marianne Islands; Malay Archipelago.

Jania, Lamouroux.

1. Jania tenella, Kütz.

Kützing, Tab. Phyc. Bd. viii., 1858, tab. 85, p. 41.

Coetivy, reef; in alcohol.

Coin Peros; in alcohol.

Praslin; in alcohol.

Seychelles; dry specimens.

Distribution. Malay Archipelago; Gulf of Mexico.

EXPLANATION OF THE PLATES.

Plate 12.

Fig. 1. *Gloiophlœa articulata*, n. sp. × $\frac{6}{5}$.
2. *Eucheuma Cottonii*, n. sp. Nat. size. Two forms.
3. *Calliblepharis prolifera*, J. Agardh. × $\frac{5}{4}$.
4. *Chylocladia perpusilla*, n. sp. × 2.
5. Fertile portion of a swollen ramulus of *Chylocladia perpusilla*. × 63.
6. *Laurencia pygmœa*, n. sp. × 2.
7. *Cladhymenia oblongifolia*. × $\frac{5}{4}$.
8. *Chondria pumila*, Vick. × $\frac{5}{4}$.
9. *Chondria simpliciuscula*, n. sp. × $\frac{5}{4}$.
10. „ „ Top of frond, with regular rows of hexagonal cells. × 80.
11. *Heterosiphonia Rendlei*, n. sp. × $\frac{5}{4}$.
12. Penicillus of *Heterosiphonia Rendlei*, with stichidia. × 24.

Plate 13.

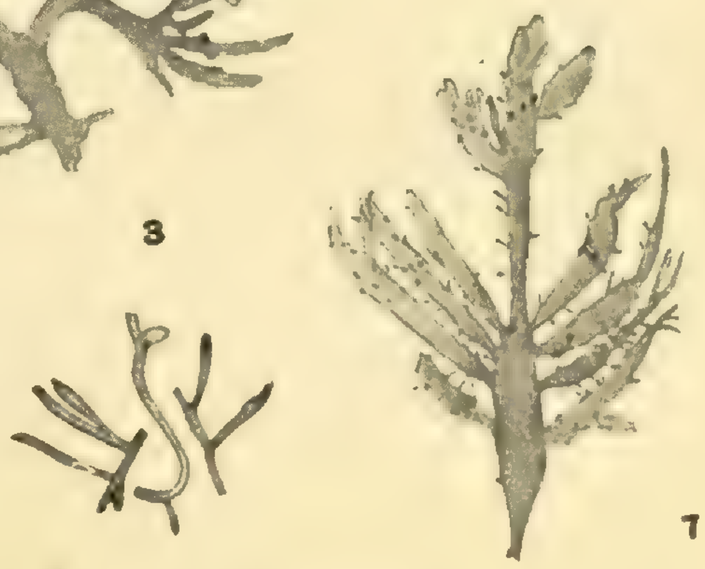
Fig. 13. *Pseudendosiphonia Gardineri*, n. gen. et sp. × $\frac{5}{4}$.
14. Top of frond of *Ps. Gardineri*. × 12. *st.*=stichidia.
15. Stichidium of *Ps. Gardineri*. × 100.
16. *Dasyopsis Stanleyi*, n. sp. × $\frac{6}{5}$.
17. *Dasyopsis aperta*, n. sp. × $\frac{5}{4}$.
18. *Dasyopsis Geppii*, n. sp. × $\frac{5}{4}$.
19. „ „ Underside of thallus, with clusters of antheridia. × 4.
20. „ „ Antheridium.
21. *Dasyopsis palmatifida*, n. sp. × $\frac{5}{4}$.
22. *Tapeinodasya Ethelæ*, n. sp. × $\frac{5}{4}$.
23. „ „ Part of frond. × 11.
24. *Amphisbetema indica* (J. Ag.). Nat. size.
25. *Galaxaura hawaiiana*, Butt. Nat. size.

Plate 14.

Fig. 26. *Gloiophlœa articulata*, n. sp. Section through apex of frond. × 32.
27. „ „ Peripheral filament, showing small cortical cells. × 340.
28. *Gloioderma ? expansa*. Nat. size.
29. „ „ Transverse section, showing large central cells. × 40.
30. *Pseudendosiphonia Gardineri*. Section through thallus. × 16. *c.*=central tube; *p.c.*=pericentral cells.
31. *Oligocladus Prainii*, n. sp. × 32.
32. *Dasyopsis aperta*, n. sp. Part of penicillus. × 46. *m.* = mother-cell of downward-growing hypha.
33. *Dasyopsis Geppii*, n. sp. Young displaced branch. × 130.
34. *Amphisbetema indica*. Apex of frond. × 24.
35. *Peyssonnelia Harveyana*. Transverse section. × 128.
36. *Peyssonnelia* ? subgen. *Ethelia*. Section through thallus; highly magnified.
37. „ Young plant, section through upper part of thallus; highly magnified.

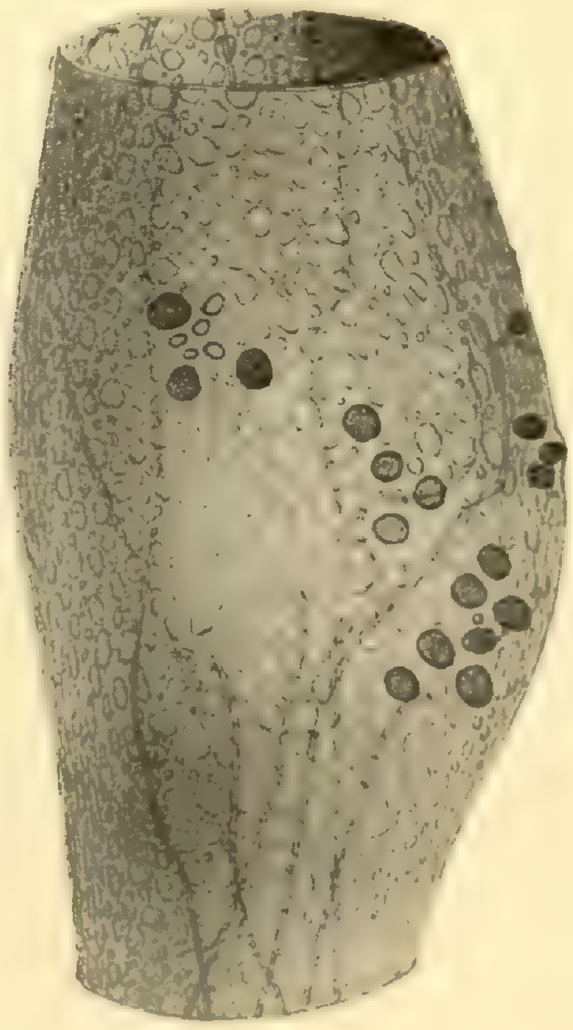
1

3



7

4

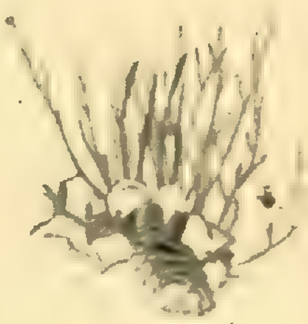


5

6

9

10



8

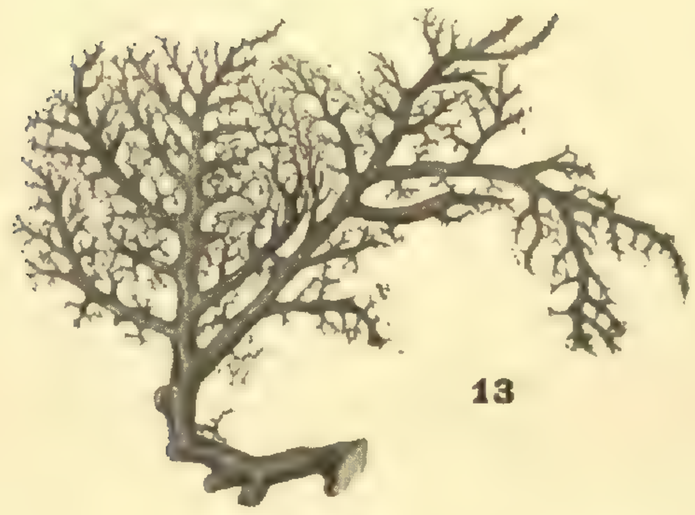
2

11

12

J. Obbes del.

MARINE ALGÆ FROM THE INDIAN OCEAN.



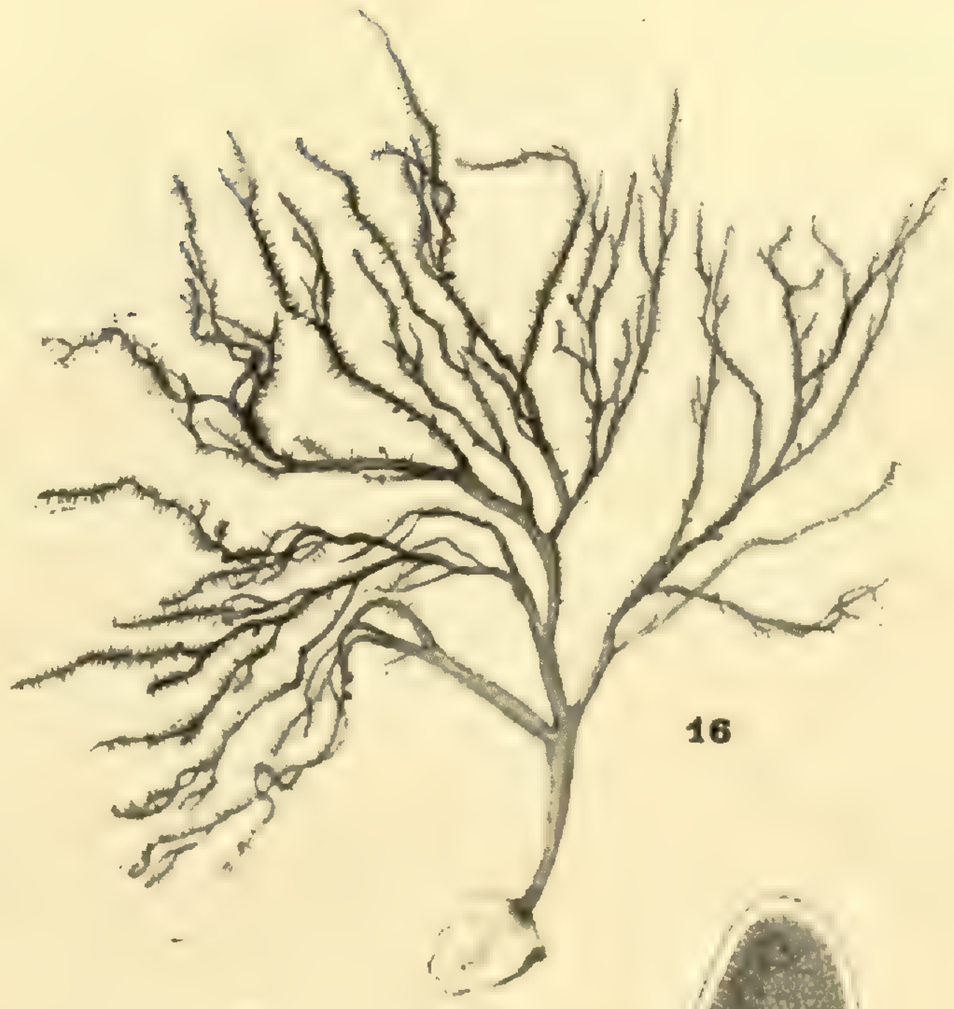
13

21

14

25

18



16

20

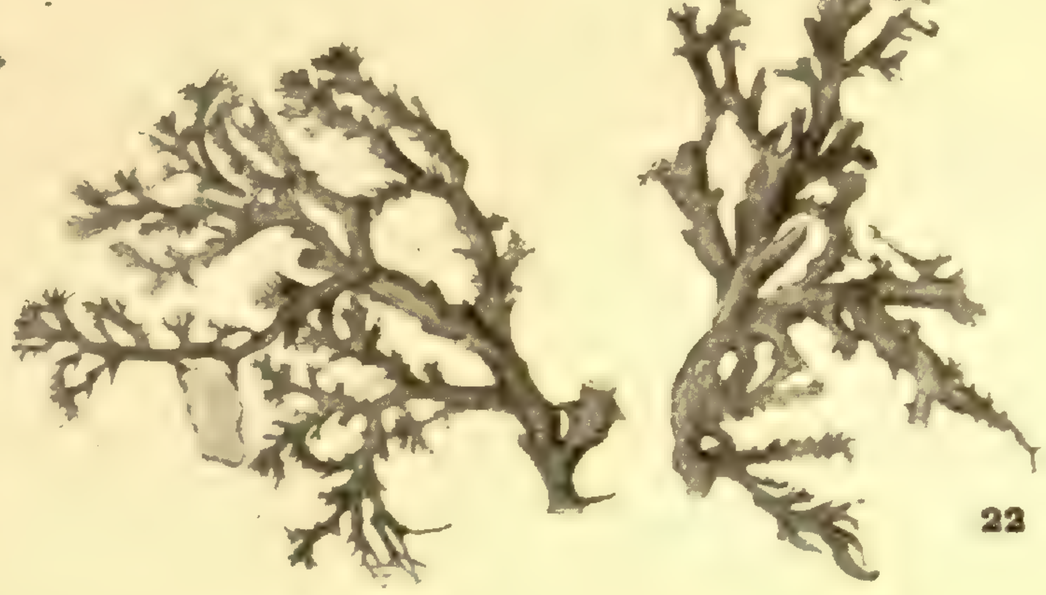
24

19

15

17

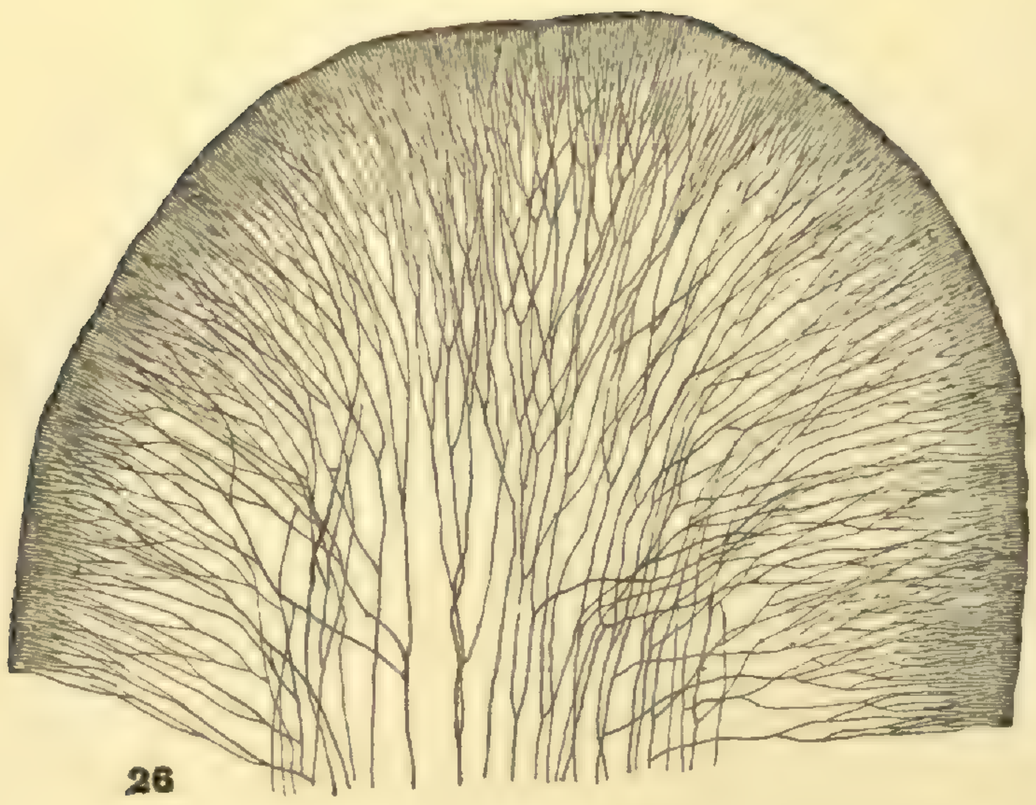
23



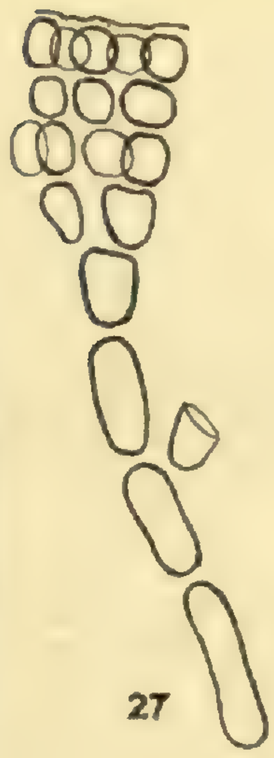
22

J. Obbes del.

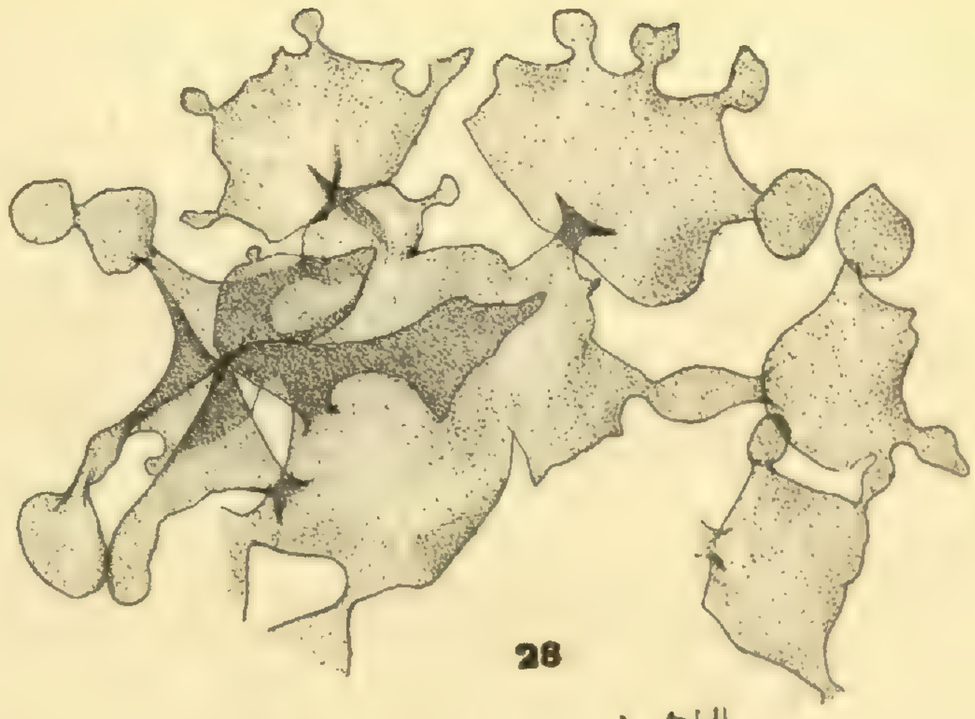
MARINE ALGÆ FROM THE INDIAN OCEAN.



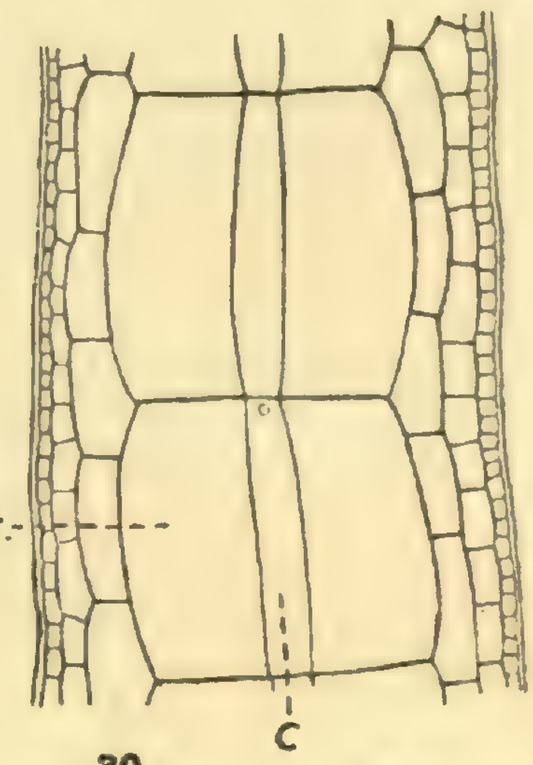
26



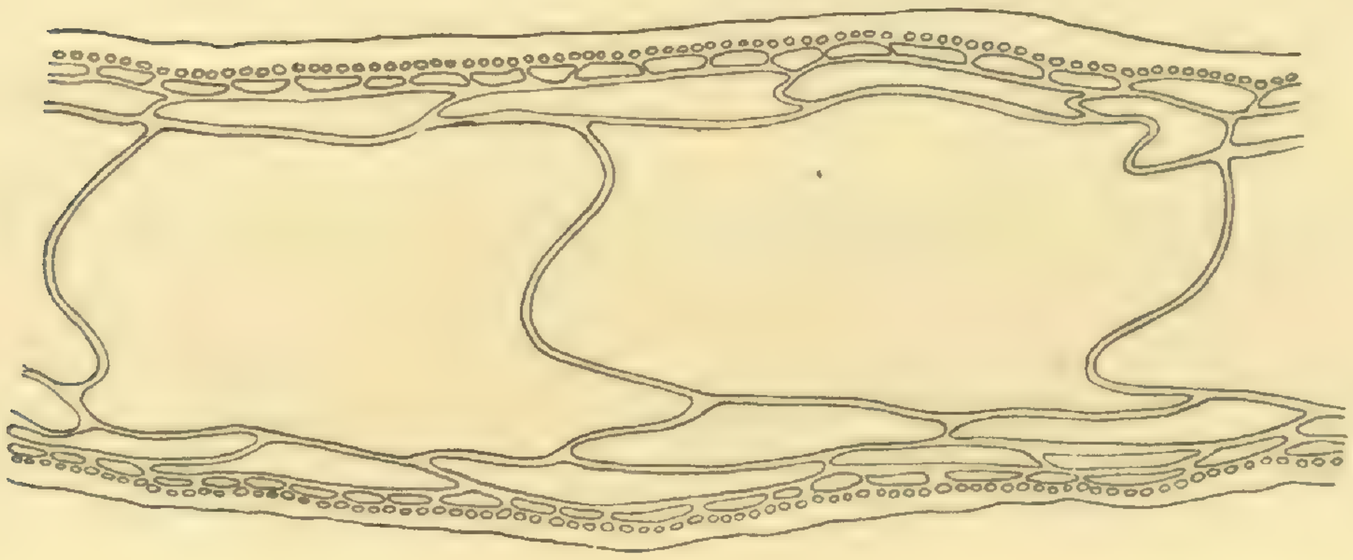
27



28



30

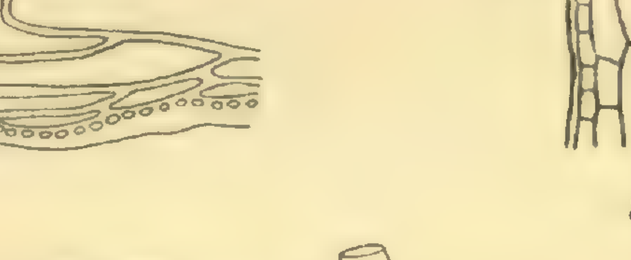


29

32

34

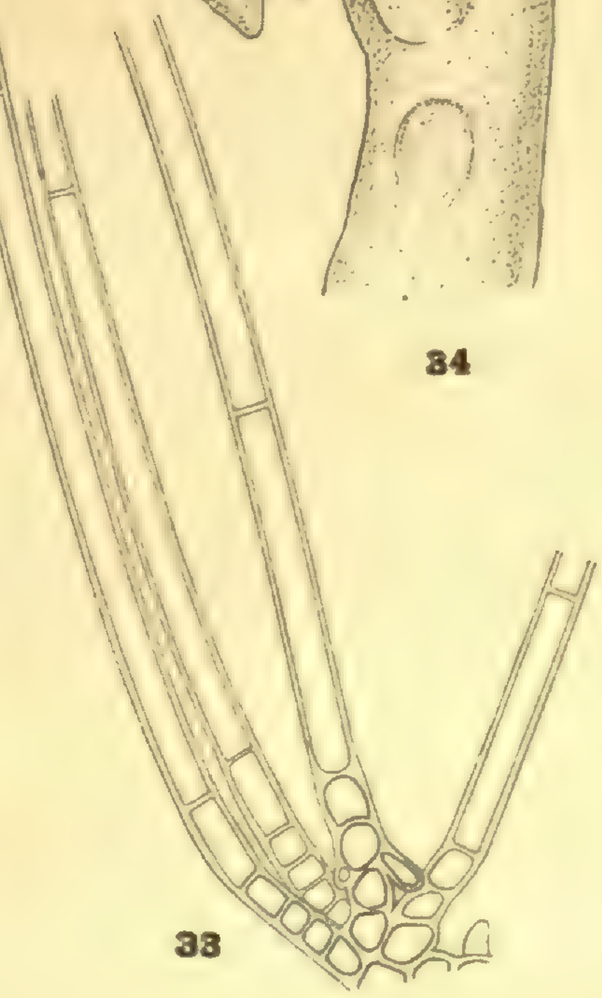
31



36

37

35



33

J. Obbes del.

MARINE ALGÆ FROM THE INDIAN OCEAN.

LINNEAN SOCIETY OF LONDON.

MEMORANDA CONCERNING TRANSACTIONS.

The First Series of the Transactions, containing both Botanical and Zoological contributions, has been completed in 30 Vols., and a few entire sets are still for sale. Only certain single volumes, or parts to complete sets, may be obtained at the original prices. The price of the Index to Vols. 1–25 is 8*s.* to the public, and 6*s.* to Fellows; to Vols. 26–30, 4*s.* to the public, and 3*s.* to Fellows.

The Second Series of the Transactions is divided into Zoological and Botanical sections. The prices of the Botanical parts of these which have been published are as undermentioned. (For the Zoological parts see Zoological wrapper.)

SECOND SERIES.—BOTANY.

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
I.	Parts I.–IX. (complete).						
	1875–80.	8	1	0	6	1	0
II.	Parts I.–XVI. (complete).						
	1881–88.	6	16	10	5	2	3
III.	Part I. 1888.	3	12	0	2	14	0
	Part II. 1891.	0	5	0	0	3	9
	Part III. 1891.	0	7	0	0	5	3
	Part IV. 1891.	0	6	0	0	4	6
	Part V. 1891.	0	6	0	0	4	6
	Part VI. 1891.	0	3	6	0	2	8
	Part VII. 1892.	0	6	0	0	4	6
	Part VIII. 1893.	0	6	0	0	4	6
	Part IX. 1893.	1	8	0	1	1	0
	Part X. 1894.	0	10	0	0	7	6
	Part XI. 1894.	0	3	4	0	2	6
IV.	Part I. 1894.	1	0	0	0	15	0
	Part II. 1894.	2	0	0	1	10	0
	Part III. 1895.	2	10	0	1	17	0
	Part IV. 1895.	0	3	4	0	2	6
V.	Part I. 1895.	0	9	0	0	6	9
	Part II. 1895.	0	12	0	0	9	0
	Part III. 1896.	0	6	0	0	4	6
	Part IV. 1896.	1	0	0	0	15	0
	Part V. 1896.	0	14	0	0	10	6
	Part VI. 1896.	0	4	0	0	3	0
	Part VII. 1897.	0	4	0	0	3	0
	Part VIII. 1897.	0	6	0	0	4	6
	Part IX. 1899.	0	12	0	0	9	0
	Part X. 1899.	0	6	0	0	4	6
	Part XI. 1899.	0	7	0	0	5	3
	Part XII. 1899.	0	12	0	0	9	0
	Part XIII. 1900.	0	1	6	0	1	2
	Part XIV. 1900.	0	3	0	0	2	3
	Part XV. 1901.	0	6	0	0	4	6

SECOND SERIES.—BOTANY (*continued*).

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
VI.	Part I. 1901.	1	10	0	1	2	6
	Part II. 1901.	0	6	0	0	4	6
	Part III. 1902.	0	18	0	0	13	6
	Part IV. 1903.	0	8	0	0	6	0
	Part V. 1903.	0	8	0	0	6	0
	Part VI. 1903.	0	12	0	0	9	0
	Part VII. 1904.	0	12	0	0	9	0
	Part VIII. 1904.	0	12	0	0	9	0
	Part IX. 1904.	0	7	0	0	5	3
	Part X. 1904.	0	14	0	0	10	6
	Part XI. 1905.	0	4	0	0	3	0
VII.	Part I. 1904.	0	5	0	0	3	9
	Part II. 1905.	0	6	0	0	4	6
	Part III. 1906.	0	3	0	0	2	3
	Part IV. 1906.	0	7	0	0	5	3
	Part V. 1907.	0	10	0	0	7	6
	Part VI. 1907.	0	4	0	0	3	0
	Part VII. 1907.	0	6	0	0	4	6
	Part VIII. 1908.	0	5	0	0	3	9
	Part IX. 1908.	0	2	6	0	2	0
	Part X. 1908.	0	7	0	0	5	3
	Part XI. 1909.	0	4	0	0	3	0
	Part XII. 1909.	0	12	0	0	9	0
	Part XIII. 1909.	0	5	0	0	3	9
	Part XIV. 1909.	0	6	0	0	4	6
	Part XV. 1910.	0	6	0	0	4	6
	Part XVI. 1912.	0	3	0	0	2	3
	Part XVII. 1912.	0	8	0	0	6	0
	Part XVIII. 1912.	0	5	0	0	3	9
	Part XIX. 1912.	0	3	0	0	2	3
	Part XX. Index.	0	3	0	0	2	3
VIII.	Part I. 1913.	1	0	0	0	15	0
	Part II. 1913.	0	8	0	0	6	0
	Part III. 1913.	0	8	0	0	6	0

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

OBSERVATIONS ON THE MORPHOLOGY AND ANATOMY OF THE GENUS MYSTROPETALON, HARV.

BY

R. J. HARVEY-GIBSON, M.A., F.L.S.,

PROFESSOR OF BOTANY IN THE UNIVERSITY OF LIVERPOOL.

LONDON:

PRINTED FOR THE LINNEAN SOCIETY

BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON-HOUSE, PICCADILLY, W.,

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

December 1913.

V. *Observations on the Morphology and Anatomy of the Genus* Mystropetalon, *Harv.*

By R. J. Harvey-Gibson, *M.A., F.L.S., Professor of Botany in the University of Liverpool.*

(Plates 15 & 16.)

Read 5th June, 1913.

In the 'Annals of Natural History,' vol. ii. no. 12, p. 385 (1839), Sir W. J. Hooker communicated a short paper by Dr. W. H. Harvey, "On two species of a new South African genus of the Natural Order Rhizantheæ of Blume," in which Harvey furnishes brief diagnoses of two species of what is now recognised as a genus of Balanophoraceæ, viz. *Mystropetalon Thomii* and *M. Polemanni*. In a memoir on "The root parasites referred by authors to Rhizantheæ, &c.", Griffith provides a more detailed diagnosis of *M. Thomii* with critical remarks, based on specimens obtained from Harvey (Trans. Linn. Soc. vol. xix. 1845, p. 303), and fourteen years later Sir J. D. Hooker, in his paper "On the structure and affinities of the Balanophoraceæ" (Trans. Linn. Soc. vol. xxii. 1856, p. 1), contributes some additional observations on the subject. Briefer references are made to the genus in Harvey and Sonder's 'Flora Capensis' (vol. ii. p. 573, 1861–2), in Bentham and Hooker's 'Genera Plantarum' (vol. iii. p. 234, 1880), and in Baillon's 'Natural History of Plants' (Engl. Ed. vol. vi. p. 505, 1880). A short account of the genus is given also by Engler (Pflanzenfamilien, III. 1. 1889, p. 252), but Marloth in his 'Das Kapland, insonderheit das Reich der Kapflora' (Wissenschaftliche Ergebnisse der deutschen Tiefsee-expedition auf dem Dampfer 'Valdivia,' 1898–99, vol. ii. pt. 3, p. 301) merely mentions the occurrence of the two species in the neighbourhood of Caledon, Cape Colony.

While on a visit to South Africa in 1905, my friend, Mrs. Solly, of Knor Hoeck, Sir Lowry's Pass, Cape Colony, told me that both species grew in or near the pass leading over the Hottentot Holland Mountains, from Sir Lowry's Pass to Caledon. I had no opportunity, during my visit, of searching for them, but Mrs. Solly kindly undertook, if possible, to obtain specimens of *M. Thomii* for me. This she was able to do, two years ago, when I received from her several specimens not only in full flower but with the rhizomes (hitherto undescribed) and the host's roots intact. Mrs. Solly described the specimens as those of *M. Thomii*, but after examination, as will be seen later, I found that they could not be referred to that species and, as I think, not even to the rarer species, *M. Polemanni*, the only description of which, so far as I am aware, is in the short paper by Harvey in the 'Annals of Natural History,' quoted above. Mrs. Solly informs me that the host roots are those of a *Protea*, although she says she had previously found *M. Thomii* parasitic on grass roots. The first time the rhizome of that

species was seen was in 1907, but it was again found in 1909. The specimens, the description of which forms the subject of the present paper, are, so far as I am aware, the first plants of this remarkable genus that have been found entire. It seemed worth while, under the circumstances, to attempt as complete a description as possible of the plant, and to present the results of the investigation to the Linnean Society, in whose Transactions the earlier accounts by Griffith and Hooker were published.

Harvey gives a brief diagnosis of the two species included by him under the genus, and distinguishes them as follows:—

"*M. Thomii*, Harv. Anterior bracteæ broadly oblong (in anthesis), one-third longer than the lateral. Limbs of the segments of the male perianth lanceolate; female perianth subglobose, obtusely tridentate."

"*M. Polemanni*, Harv. Anterior bractea spathulate, with a narrow claw. Limbs of the segments of the male perianth elliptical, very concave; female perianth tubular, trifid."

In addition, Harvey's figure of *M. Polemanni* shows the scales on the upper part of the flowering axis as being ciliate along their margins, while those of *M. Thomii* are smooth.

Harvey gives as the habitat of *M. Polemanni*, "at Hoouw Hoch Pass, Mrs. Denys, who communicated the only specimen yet seen to Polemann, from whom I received it."

The specimens sent to me were collected on March 25th, 1910, near Caledon, growing on rough rocky ground, in a very exposed situation on the side of a hill. Mrs. Solly informs me that on the day after her visit to the locality "a veldt fire reduced the hill-side to a blackened waste." It would seem, therefore, that the chances of obtaining many more specimens of the plant at present under consideration are very remote.

Historical Summary.

The inflorescence of *Mystropetalon* is described by Harvey as consisting of a thick fleshy axis covered by linear scales and ending in a spike 3–4 inches in length, densely covered with male flowers above and female flowers below. The male flower is surrounded by three bracts, the anterior of which is oblong in *M. Thomii* and spathulate in *M. Polemanni*, while the two postero-lateral bracts are more or less united and considerably smaller. All the bracts are ciliate along their margins and keels. The perianth in both species is tripartite, the two posterior parts being more or less united above, while the anterior part is free almost to its base, where it fuses with the two posterior lobes. All the perianth parts are spathulate. Harvey figures two stamens "opposite to and inserted on the posterior segments of the perianth," each with versatile anthers and cubical pollen grains "with fluted angles." In the centre of the male flower lies a "minute abortive ovary."

The female flower is described also as having three bracts, but here the postero-lateral segments are larger than the anterior in *M. Thomii*, but considerably smaller than in *M. Polemanni*. The perianth is described as trilobed and epigynous and from the

centre arises a filiform style. The ovary in both species is "ellipsoidal, attenuated at the base," and contains, in *M. Thomii*, "a fleshy mass (without distinction of ovules)" and is surrounded by an arilloid "torus." Harvey was thus unable to distinguish either ovule, seed, or embryo, although he figures what is, apparently, intended to represent an embryo in *M. Polemanni*.

Griffith (Trans. Linn. Soc. xix. 1845, p. 337) gives a rather fuller description of *M. Thomii* from specimens sent him by Harvey. He states that there are three stamens in the male flower, one (when present) rudimentary attached to the anterior "sepal." He also mentions the occurrence of two abortive stamens in the female flower. The style is described as trisulcate and the stigma as trilobed. Griffith refers to a doubtful embryo (the word is followed by a note of interrogation) *centrally* placed and separated from the "epicarpium" by a spongy cellular tissue. Probably Griffith did not see the embryo at all, for its position is apical, not central, and it is so small that it might well escape notice unless investigated by means of serial microtome sections. Indeed, in his appended observations he speaks of the "central tissue of the fruit" as "not separable as one body, breaking up rather on the slightest pressure occasioned by attempts at dissection." "In this respect," he adds, "it differs considerably from the embryo of *Balanophora* and *Phæocordylis*." Later on he speaks of it as a "sporuliferous mass." He does not mention *M. Polemanni* at all.

Hooker (Trans. Linn. Soc. xxii. 1859, p. 31) draws attention to Harvey and Griffith's failure to find the real embryo and describes it in *M. Thomii* "at the upper part of the seed, lying quite loose in its axis, with the radicle pointed to the hilum and close to it." The "sporuliferous mass" referred to by Griffith is, according to Hooker, "albumen." In the 'Flora Capensis' (vol. ii. p. 573), Harvey and Sonder apparently accept Hooker's interpretation, for they describe the fruit as one-seeded with a "thin juicy epicarp and a crustaceous endocarp," while the embryo is stated to be "very minute in the base of easily friable albumen." Bentham and Hooker (Gen. Pl. iii. p. 235) state with greater accuracy that the embryo is apical. Engler (Pflanzenf. III. 1. p. 252) adds one item of interest with reference to the structure of the ovary (under generic characters). He describes it as containing three ovules arising from a free placenta, each being reduced to an embryo-sac.

Beyond brief references to the genus in a few other systematic works, I know of no further published accounts dealing with the subject of the present memoir.

The Rhizome and its Relation to the Host Plant.

No description of the morphological and anatomical features of the subterranean parts of either species of *Mystropetalon* has, so far as I am aware, ever been published; all the authorities quoted, when they mention its rhizome at all, describe it as "unknown." The first time it was found was, as above stated, in 1907, but whether these specimens were really those of *M. Thomii* or of the present plant, I am unable to say, although, probably, as they were seen by Dr. Marloth, they were of *M. Thomii*. If that be so,

then the first rhizomes of the plant, whichever it is, under investigation, to be gathered are those on which the present observations have been made.

The rhizome is *usually*, as I am informed, parasitic on the roots of a *Protea*, and the material in my possession shows rhizomes in several stages of development.

A fully adult rhizome has the appearance of a very nodular, irregular mass, about 40 mm. in diameter, closely investing the root of the host. Such a rhizome is figured in Pl. 15. fig. 1, while fig. 2 shows younger rhizomes in various stages of development, one of them beginning to give origin to two erect flowering shoots.

Anatomically, the rhizome is covered with a layer of irregular thickness composed of cutinised cells without intercellular spaces, forming a superficial cork. The main mass of the rhizome is composed of fairly large parenchymatous cells, the majority of which contain a substance which I at first presumed to be related in chemical composition to the resinous material described as "balanophorin" by Goeppert (Verh. K. Leop.-Car. Akad. d. Nat. vol. xviii.) in *Balanophora*. Cells containing this deposit are scattered all through the rhizome, but are specially abundant in the cortex and mixed with the vascular tissue (figs. 5 & 6). An attempt was made to determine the chemical nature of the brown deposit, which amounts to about 50 per cent. by weight of the dried rhizome, but only negative results were obtained. Since the substance is insoluble in ether, alcohol, and benzene, and does not burn readily, it may be concluded that it is neither a resin nor a wax. It is unaffected by boiling in water and the solution gives no reducing-sugar tests. The possibility of its being a glucoside is excluded by the fact that it is insoluble after boiling for three minutes in dilute sulphuric acid. It gives none of the reactions of protein. It is not affected by strong sulphuric acid in the cold, but the powdered rhizome gives, on standing, a vigorous reaction to Molisch's test. One is thus forced to the conclusion that it has relations with the carbohydrates. It gives no reaction to iodine nor to iodine and sulphuric acid. It cannot be a simple carbohydrate, but is probably a peculiar carbohydrate of the cellulose group. The Molisch test when repeated under the microscope was not entirely satisfactory, for the substance took on not a violet but a deep red-brown colour. Unfortunately, the amount of tissue at my disposal was too limited to permit of a detailed quantitative analysis. For convenience I shall speak of the substance in the course of this paper as "mystrin," for if Goeppert and Poleck's determination of the corresponding substance in *Balanophora* as a wax or resin be correct it is certainly not "balanophorin."

It was found to be quite impossible to determine any definite arrangement of vascular bundles in the rhizome owing to its extremely wrinkled and irregular form. Bundles of short tracheids with reticulate thickenings, almost verging on spiral, wander irregularly through the ground parenchyma. These strands are accompanied, usually, but not always, by elongated elements obviously with sieve-tube characters. Many of the tracheids may be described as scalariform, although Solereder ('Systematic Anatomy of Dicotyledons,' vol. ii. p. 739) doubts the presence of such elements in the Balanophoraceæ, although this is asserted by Eichler. Fig. 5 shows such "scalariform" tracheids mingled

with "mystrin" parenchyma taken from the rhizome just above the point of origin of the haustorium, while fig. 6 shows the short reticulate xylem elements accompanied by "mystrin" cells and elongated nucleate phloem parenchyma. Accompanying these elements were chains of cells with large nuclei resembling those described by Pierce in *Brugmansia*, *Rafflesia*, and *Balanophora* (Ann. Bot. vol. vii. 1893), but the mode of preservation of the material did not permit of the determination of the ultimate connection of the cells of the haustorium with those of the host.

The Inflorescence.

The inflorescence is a clavate spike from 80 to 100 mm. in length by about 20 mm. in diameter near its apex (Pl. **15**. fig. 1). The axis tapers to its point of origin from the rhizome, and is covered for two-thirds of its length with closely-set linear leaves, while the upper third bears female and male flowers in two distinct zones, the former occupying the lower, the latter the upper portion of the floral area.

The leaves are rather pointed in the basal region of the axis, but become more truncated as the floral region is approached. They are arranged in a dense spiral and are of a bright red-brown colour due to the abundant deposits of "mystrin." The leaves have broad bases, are relatively thick centrally, and bordered by thin wings. The abaxial surfaces, as well as the margins, are densely covered with long unicellular hairs, but the median region of the adaxial side is quite glabrous. There is one median vascular cord consisting of a variable number of short, more or less irregular, reticulate and spiral tracheids, which lie immediately below the adaxial epidermis, accompanied by a very small-celled phloem. As in the case of the rhizome, "mystrin" cells are interspersed among the vascular elements. The main mass of the leaf consists of spherical and polygonal parenchyma with thick pitted walls and with small intercellular spaces; most of these cells contain "mystrin." The epidermis, which consists of cubical or polygonal cells, is destitute of stomata (fig. 11).

Fig. 7 (Pl. 15) shows a transverse section of the axis taken at the level of the origin of vegetative leaves. The superficial cells (fig. 8) are completely filled with "mystrin" and are comparable in size and general appearance with those of the body of the axis as a whole. Many of these fundamental cells are also more or less filled with the same brown deposit. The vascular bundles are twenty to thirty in number and are distributed quite irregularly through the ground-tissue. These bundles have apparently no cambium, and in all cases show cells filled with "mystrin" interspersed among the vascular tissue elements proper. At fig. 9 (Pl. **16**) one of the smaller bundles is figured, and it will be seen that it consists of a number of tracheids, some of which have spiral, others reticulate thickenings, while the phloem consists of thin-walled, elongated, nucleated elements resembling phloem parenchyma. No sieve-tubes, exhibiting definite sieve-plates, could be distinguished. The larger bundles have several patches of tracheids and several patches of phloem cells more or less separated by larger, thin-walled parenchyma containing "mystrin" (fig. 10).

The Male Flowers.

The male flowers, when young, are arranged in closely-packed alternating whorls, which gradually open out as maturity is reached. The central axis cells are loaded with "mystrin," as are also the cells of the bracts and perianths. Within the perianth-lobes lie the anthers of the two stamens, whose connectives are also surrounded by cells containing the same brown deposit. The male flower (fig. 13) is surrounded at its base by three bracts. One of these, anterior in position, is stalked, with a spathulate lamina, and covered with long unicellular hairs on the abaxial side. There is a single central vascular bundle as in the axis-leaves, and all the cells of the ground-tissue are filled with "mystrin." The latero-posterior bracts are very much smaller and more scale-like, sessile, and fused for a certain distance upwards from their point of origin. These bracts are also furnished with unicellular hairs along their margins and on their posterior surfaces. Within the bracts and arising opposite to them are three perianth segments which are fused at their bases to form a very short cup. The perianth segments are nearly twice the length of the anterior bract. The anterior segment is slightly shorter than the two posterior segments and stands apart from them. It has a single median vascular bundle running through the slightly convexo-concave claw and is continued unbranched into the concave spoon-shaped lamina. The perianth segments are only slightly concave, and resemble exactly the figures given by Harvey (Ann. Nat. Hist. ii. tt. 19, 20) for those of *M. Thomii*. All the cells, both of claw and limb, are filled with "mystrin." Griffith (Trans. Linn. Soc. xix. p. 337) in his description of *M. Thomii* says, "stamen tertium, dum adest, rudimentarium, adnatum ungui sepali tertii antici." I have examined over a hundred male flowers of the plants in my possession, but I have never found the slightest trace of any such third stamen. The posterior perianth segments have free claws, but the limbs are united above. They are similar in form and histological structure to the anterior segment, and have also concave limbs forming a covering to the two functional stamens. The stamens arise just where the claw broadens out into the limb, and the filament is inserted on the anther about half-way up its length. Harvey (*l. c.* p. 386) describes the anthers as *versatile*, but Griffith and Hooker speak of them as *extrorse*. As a matter of fact, in the unripe flower the anthers *are* extrorse, but as the flower opens the anther becomes versatile and ends by being *introrse*, owing to a complete inversion of position of the anther with reference to the axis of the flower.

The anther is markedly bilobed and the lobes open by longitudinal dehiscence. The cells of the filament, including the vascular bundle, are full of "mystrin," and several layers of cells surrounding the connective also contain the same deposit. The wall when ripe is composed of one layer of cells, and the walls of these cells show the usual rib-like thickenings common in anther-walls, save in the region of longitudinal dehiscence (fig. 14). The pollen grains, as described by Harvey, are cubical as a rule, though some are pentagonal or, rarely, hexagonal (fig. 15). Harvey figures the angles of the grains as

fluted, but I have not been able to distinguish any such indentations. In most grains one prominent nucleus is visible, although two can be made out in some of the larger grains.

At the bottom of the shallow cup formed by the fusion of the bases of the perianth segments, there occurs a parenchymatous protuberance, the cells of which resemble those of the "arilloid" swelling which surrounds the base of the ovary. This protuberance is continued into a short projection whose cells are filled with "mystrin." This probably represents the rudimentary ovary mentioned by Harvey and by Griffith, but none of my sections exhibits any indication of distinct ovarial structure (fig. 16).

The Female Flower.

Descriptions of the female flower of *M. Thomii* alone are given by Griffith and Harvey, the latter of whom only figures it; Harvey also figures the female flower of *M. Polemanni* but gives no account of it. Harvey's drawings show, approximately, equal bracts, ciliate along the margins, and the anterior segment with a hairy external median ridge. Centrally placed (in *M. Polemanni*) lies a swollen, cup-shaped wrinkled "torus" from which springs the ovary, bearing at its apex a minute, trifid, tubular perianth, and a long style, without any prominent stigma. Harvey figures the bracts of *M. Polemanni* both in "anthesis" and in the fruiting condition as approximately of the same length, the anterior bract narrowing to its base and covered with hairs, while the latero-posterior bracts are broader and only marginally ciliate. The bracts of the female flower of *M. Thomii*, on the other hand, are, according to Harvey's figures, of equal length in anthesis, but, in the fruiting condition, the latero-posterior bracts are represented as about twice the length of the anterior bract. Again, the perianth of the female flower of *M. Thomii* is an almost spherical cup, with a trilobed margin, contrasting, in this respect, with the narrow, tubular, trifid perianth of *M. Polemanni*. Harvey also figures the ovary as basally pointed, the basal projection rounded off and seated in the central depression of the "torus." Griffith describes the ovary of *M. Thomii* as "globosum, parce puberulum, basi attenuata"; Harvey also mentions the "minutely hispidulous" character of the wall of the ovary.

As my own observations differ in some respects from those of Harvey, it may be more convenient to describe the whole flower *de novo*. The description, it may be prefaced, is that of a flower whose ovule had been fertilised, although the style was still present at the apex of the ovary.

The flowers are apparently proterogynous, for in those inflorescences which had mature male flowers with anthers still closed or in the act of dehiscing, the female flowers had lost their styles and perianths, and the ovary had become transformed into a small, almost black fruit with a sclerotic pericarp. In the single younger inflorescence amongst my material the male flowers were still immature, while the bracts of the female flowers already enclosed young fruits but with styles still attached.

In a letter from Mrs. Solly, accompanying the specimens, she makes an interesting observation on the pollination of *Mystropetalon*. My correspondent writes as follows:—

"The female flowers open first. I found bees visiting the flowers in the orthodox manner; I caught one and found it covered with pollen. This point I had not been able to fix before."

As already stated, the youngest female flower I could find contained an ovary whose ovule had obviously been fertilised. The flower is surrounded, as in the case of the male, by three bracts, the anterior being pointed linear and about one-fourth longer than the two latero-posterior, which are pointed ovate. The anterior bract bears very numerous unicellular hairs both over the abaxial surface and along the margins, while the latero-posterior bracts are ciliate on their margins only. Arising centrally is a circular, transparent disc ("torus" of Harvey), from the cup-like depression in which arises the ovoid or elliptical "ovary" bearing apically a long filiform style. Just at the junction of the ovary and style springs the extremely small cup-shaped perianth (figs. 17 & 18). I have examined very many flowers and never found the tubular, trifid form of perianth figured for *M. Polemanni* by Harvey. The form of the perianth, on the other hand, invariably resembled that figured by the same author for *M. Thomii*. The margin of the perianth was, however, not trifid, but was subdivided into six or more lobes of approximately equal size. Finding this deviation from Harvey's figures of the perianth of *M. Polemanni*, I at first thought that my material might include both species, but that this was not the case was shown by an examination of male and female flowers from the same inflorescence. It will be noted in the diagnoses of the two species given by Harvey that that author separates *M. Thomii* from *M. Polemanni*, on the ground that the former has "anterior bracteæ broadly oblong" with a "subglobose, obtusely tridentate" female perianth and "somewhat concave" laminæ in the male perianth, while *M. Polemanni* has its "anterior bractea (in the male flower) spathulate with a narrow claw" and with "very concave" laminæ in the segments of the perianth, while the female perianth is "tubular, trifid." The present material seems to combine these characters, for the male flowers have, on the whole, the characters of *M. Polemanni*, while the female flowers resemble more closely those of *M. Thomii*. (The question of identification is discussed below.)

The perianth cup has a vascular supply consisting of a few very delicate spiral and reticulate tracheids arranged in two or three strands, and the rather regularly arranged oblong cells of which the perianth is mainly composed are filled with "mystrin." Arising from the base of the perianth cup towards its posterior side are two small parenchymatous nodules representing the pair of abortive stamens mentioned by Griffith (fig. 18). They show no histological differentiation and are not present in all flowers. No trace of an anterior stamen could be made out after examination of several hundred serial sections of female flowers. The ovary is elliptical and sparsely covered with small unicellular hairs, which apparently drop off soon after fertilisation, for slighter older fruits are quite glabrous. No hairs occur on the perianth. From the base of the perianth cup arises the relatively long filiform style. It is considerably constricted at its point of origin from the ovary (fig. 18), but expands to its normal diameter before reaching the rim of the perianth; thereafter it maintains a uniform

thickness and finally ends in a papillose stigma which in most cases shows subdivision into three more or less well-marked lobes. Harvey's figures of the female flowers of *M. Polemanni* do not show any prominent stigma at all. Usually three delicate vascular bundles pass up the style ending in a brush-like tuft of reticulate tracheids in each of the stigmatic lobes (fig. 19). The style is composed of oblong parenchyma full of "mystrin," but I have been unable to see any indication of the three grooves mentioned by Griffith—though it is possible that these may be visible in the fresh condition. On tracing the course of the bundles down the style it is found that they anastomose from time to time, sometimes splitting into four or even five bundles and then reuniting, finally fusing into two larger bundles in the constricted region just inside the perianth. At the point of origin of the perianth these strands give off two or sometimes three chains of very delicate spiral tracheids, which enter the perianth, while the main strands break up into several fine branches which pass down through the inner layer of the ovarial wall, finally uniting again into one larger bundle in the conical base of the ovary, where, after passing through the torus, it unites with the vascular system of the axis of inflorescence.

The Fruit.

The fruit remains enclosed within the persistent and accrescent bracts, its base surrounded by the almost colourless swollen disc ("torus" of Harvey). The perianth and style are deciduous, leaving a ragged scar at the apex of the fruit. The ripe fruit is orange-shaped and about 2 mm. in diameter, and of a deep brown-black colour. It tapers rapidly to its point of attachment in the swollen receptacle. In form it much more closely resembles the fruit of *M. Thomii* as figured by Harvey than it does the oblong elliptical fruit of *M. Polemanni*. The pericarp (fig. 20) consists externally of a double layer of flattened cells whose cavities are completely filled with "mystrin," thus accounting for the intense brown-black colour of the fruit as seen with the naked eye. These layers are followed internally by two layers of very thick-walled sclerotic cells, deeply pitted and partly filled with "mystrin." Then follows a layer of polygonal or oblong cells, rather loosely arranged, merging into a layer of more elongated cells, among which run the delicate vascular strands already referred to. All of these cells are filled with "mystrin." The pericarp encloses a mass of large polygonal cells whose outermost layer is in the form of smaller and more flattened plates. These cells possess large nuclei and finely reticulate and vacuolated protoplasmic contents which take on a deep stain with the usual anilin dyes. This tissue, obviously endosperm, has no "mystrin" in its cells, and for that reason is sharply marked off from the pericarp.

Engler (Pflanzenfamilien, III. 1. 252) describes the fruit as "nussartig, mit fleischigem Epicarp, dünn krustigem Mesocarp und dünnwandigem Endocarp." In no case have I seen any evidence of "fleshiness" in the external layers of the fruit-wall. Indeed, sectionising the fruit is a matter of some difficulty owing to the brittleness of the external wall. As Engler makes no mention of the fleshy disc subtending the fruit,

one is led to conclude that by "fleshy epicarp" he means to indicate this disc; but seeing that it arises below the ovary and is quite independent of it (fig. 21), and further, never reaches more than a quarter of the distance up the exterior of the fruit, it is impossible to accept such an interpretation of its nature. If a differentiation into distinct layers in the fruit-wall is to be recognised at all, then the three layers indicated above must stand for epi- meso- and endocarp respectively, and the succulent "torus" must be regarded as an accessory development from the peduncle above the point of origin of the bracts, analogous to that seen on a much larger scale in such fruits as *Anacardium*.

None of the female flowers in my material was young enough to enable me to confirm or refute Engler's statement that there are three ovules in the ovary, each reduced to an embryo-sac. There is certainly no confirmatory evidence to be obtained from an examination either of the young or mature fruits.

The fruit is connected with the axis of inflorescence by an attenuated stalk composed centrally of small deeply stainable parenchyma, through which runs the vascular cord supplying the pericarp and style. These vascular elements are surrounded by several patches of "mystrin" cells. From this axis arises a massive swollen ring of large, thin-walled parenchyma with little or no contents in the cells, forming the torus. It is covered externally by a single strongly cutinised layer of flattened cells whose contents stain deeply. The fleshy disc adheres to the fruit when ripe, separation occurring at its junction with the axis of inflorescence.

The embryo was first made out by Hooker in *M. Thomii*, who figures it as a minute pear-shaped body imbedded in endosperm at the apex of the fruit, just below the point of origin of the style. My sections confirm this position, but show an obconical embryo composed of uniform undifferentiated parenchyma lying in a minute cavity in the relatively large-celled endosperm (fig. 21). None of my sections show any indications of a placenta or funicle, nor does the seed possess anything in the way of a testa.

Identification.

As I have pointed out in the preceding pages, the plants on which the above observations were made do not appear to conform strictly with Harvey's diagnosis of either of the two species named by him. In some respects they resemble *M. Thomii*, in other respects they suggest *M. Polemanni*, while in yet others they agree with neither of these species. Sir David Prain informs me that specimens had been sent to Kew by Mr. Bolus and labelled *M. Thomii*, but that all of them on examination agreed with Harvey's drawings of *M. Polemanni*.

The following tabular statement shows the points of agreement and difference between Harvey's descriptions and figures as compared with the characters shown by the material on which the present paper is based.

M. Thomii.	M. Polemanni.	Present Material.
Male flower.	*Male flower.*	*Male flower.*
1. Anterior bract oblong.	1. Anterior bract spathulate.	1. Anterior bract spathulate.
2. Posterior bracts $\frac{2}{3}$ length of anterior bract.	2. Posterior bracts $\frac{1}{2}$ length of anterior bract.	2. Posterior bracts $\frac{1}{4}$ length of anterior bract.
3. Anterior perianth lobe rather shorter than posterior.	3. Anterior perianth lobe $\frac{2}{3}$ length of posterior lobes.	3. Anterior perianth lobe rather shorter than posterior lobes.
4. Perianth laminæ slightly concave.	4. Perianth laminæ very concave.	4. Perianth laminæ slightly concave.
5. Pollen cubical with fluted angles.	5. Pollen cubical with fluted angles.	5. Pollen cubical or pentagonal without fluted angles.
Female flower.	*Female flower.*	*Female flower.*
6. Anterior bract oblong.	6. Anterior bract rather spathulate (in fig.).	6. Anterior bract lanceolate.
7. Posterior bracts much longer than anterior in the fruiting state.	7. Posterior bracts equal to anterior.	7. Posterior bracts shorter than anterior.
8. Perianth subglobose or ellipsoid.	8. Perianth tubular.	8. Perianth subglobose or campanulate.
9. Perianth margin 3-lobed.	9. Perianth margin markedly trifid.	9. Perianth margin multifid.
10. Ovary ovoid.	10. Ovary oblong.	10. Ovary ovoid.
11. Stigma discoid.	11. Stigma not swollen.	11. Stigma trilobed.

In point 1 only my material agrees with *M. Polemanni*; in points 3, 4, 8 and 10 it agrees with *M. Thomii*; in points 2, 5, 6, 7, 9 and 11 it agrees with neither.

I was able, through the kindness of Professor H. Dixon, F.R.S., of Trinity College, Dublin, to explore Harvey's Herbarium housed there, but unfortunately we were unable to find the type-specimens, and since my return Professor Dixon writes me to the effect that after another thorough investigation he has failed to discover them. Under the circumstances, and seeing that my material as above described, cannot be said to be either of Harvey's species, I am obliged to consider my plants as belonging to a new species, to which I would desire to give the name of *M. Sollyi* in recognition of its collector, Mrs. Solly, of Sir Lowry's Pass, Cape Colony, with the specific characters given in the above table.

Bibliography.

Harvey, W. H.—"On two species of a new South African genus of the Natural Order Rhizantheæ of Blume." Annals of Natural History, vol. ii. no. 12 (1839) pp. 385–388, tt. 19, 20.

Griffith, W.—"On the Root Parasites referred by authors to Rhizantheæ; and on various plants related to them." Trans. Linn. Soc. vol. xix. (1845) pp. 303–347, tt. 34–39.

Hooker, J. D.—"On the Structure and Affinities of the Balanophoraceæ." Trans. Linn. Soc. vol. xxii. (1856) pp. 1–68, tt. 1–16.

Harvey, W. H., & O. W. Sonder.—Flora Capensis, vol. ii. 1861–2, p. 573.

Bentham, G., & J. D. Hooker.—Genera Plantarum, vol. iii. pt. 1, p. 234.

Baillon, H.—Natural History of Plants. Eng. Ed., vol. vi. p. 505.

Engler, E.—Pflanzenfamilien, vol. III. i. (1889) p. 252.

Marloth, R.—"Das Kapland, insonderheit das Reich der Kapflora." Wiss. Ergeb. d. deut. Tiefsee-expedition auf dem Dampfer 'Valdivia,' 1898–99, vol. ii. pt. 3, p. 301.

Goeppert, H. R.—"Ueber den Bau der Balanophoreen." Verh. Leopold.-Carol. Akad. d. Nat. xviii. Supp. 1, 1841, pp. 231–272, tt. 1–3.

Solereder, H.—Systematic Anatomy of the Dicotyledons, vol. ii. (1908) pp. 738–739.

Pierce, G. J.—"On the Structure of the Haustoria of some Phanerogamic parasites." Ann. Bot. vol. vii. (1893) pp. 291–327, tt. 13–15.

EXPLANATION OF THE PLATES.

Plate 15.

Fig. 1. Rhizome and flowering axis of *Mystropetalon Sollyi*, n. sp., showing attachment to root of *Protea* sp. (nat. size).

2. Young rhizomes, in various stages of development, on a *Protea* root (nat. size).

3. Transverse section of a young *Protea* root (P) with the rhizome and haustorium of *Mystropetalon*. *x*, xylem and *s*, sclerotic fibres in host root. (× 16.)

4. Transverse section of a *Protea* root with entering haustorium. Centrally the deformed xylem of the host root; *b*, "mystrin" cells; *bf*, bast fibres of host root; *s*, sclerotic tissue of the cortex; *ck*, cork layer; *p*, phloem parenchyma and sieve-tubes of the haustorium; *x*, tracheids of the haustorium. (× 60.)

5. Tracheids mingled with "mystrin" cells from the haustorium. (× 350.)

6. Tracheids (reticulate), "mystrin" cells, and phloem elements from the rhizome. (× 550.)

7. Transverse section of the base of the flowering axis (× 16); *a*, vascular strand; *b*, "mystrin" cells. (× 16.)

8. Superficial layers of the stem cortex showing the "mystrin" deposits. (× 550.)

Plate 16.

Fig. 9. Transverse section of one of the smaller vascular bundles of the flowering axis. *b*, "mystrin" cells; *x*, xylem; *ph*, phloem. (× 550.)

10. Transverse section of one of the larger vascular bundles of the flowering axis (lettering as in fig. 9). (× 250.)

11. Transverse section of one of the scale leaves. (× 60.)

12. Longitudinal section of one of the vascular strands of the floral axis, showing xylem elements, phloem, and "mystrin" cells. (× 550.)

13. Male flower. (× 35.)

14. Section of the wall of the anther with pollen grains. (× 350.)

15. Pollen grains, six- and seven-sided. (× 550.)

16. Abortive ovary of the male flower. (× 350.)

17. Female flower. (× 60.)

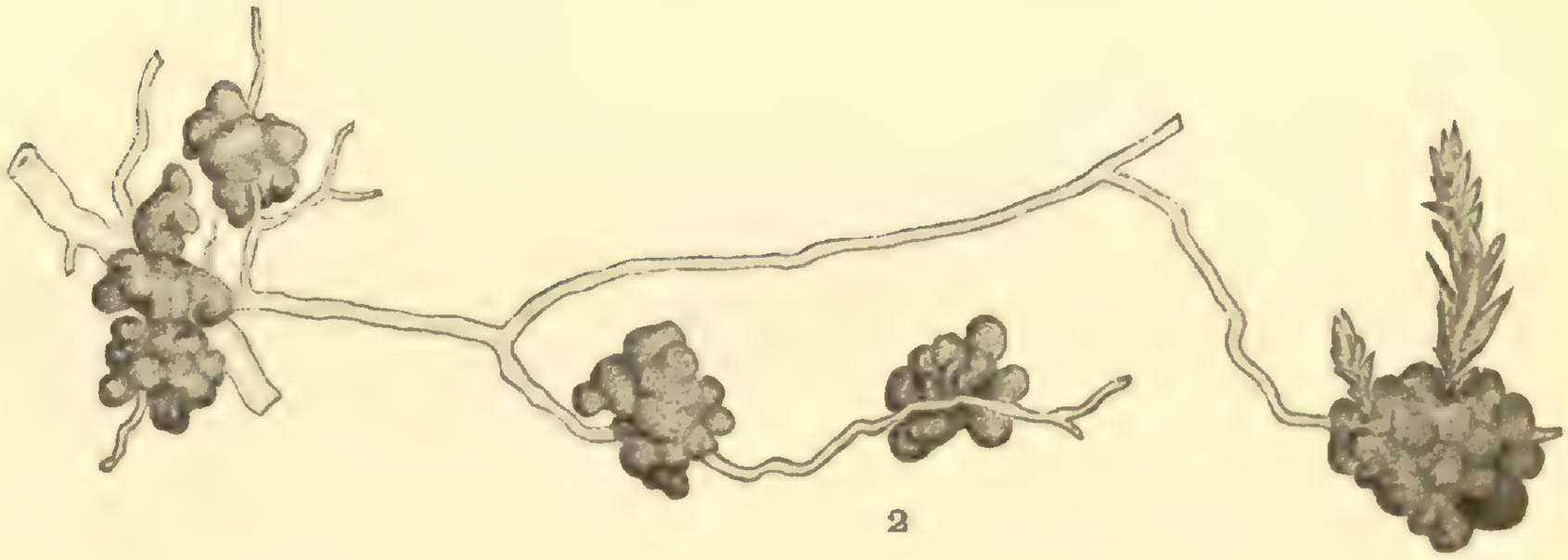
18. Longitudinal section of the perianth and style of the female flower, showing abortive stamens (semidiagrammatic).

19. Trilobed stigma. (× 350.)

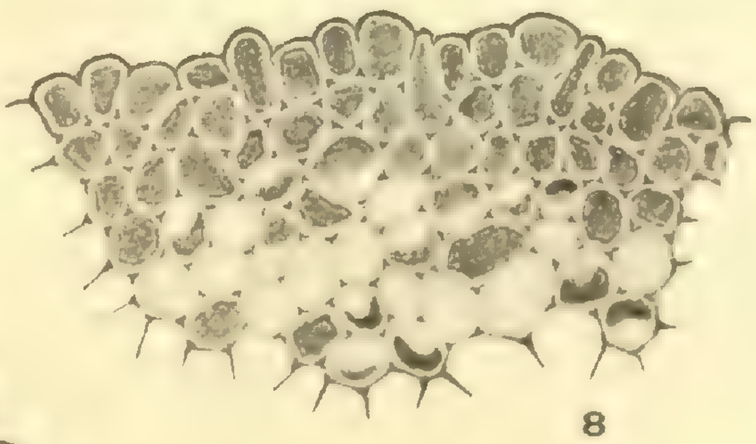
20. Transverse section of fruit-wall and portion of the endosperm. (× 550.)

21. Longitudinal section of the fruit, showing the "torus," fruit-wall, endosperm, and embryo. (× 60.)

1

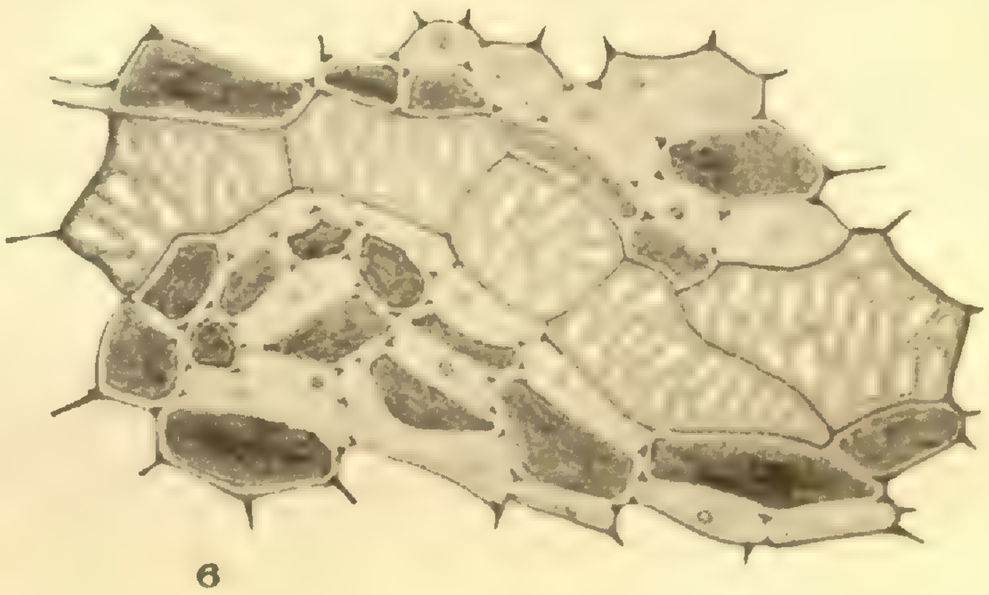


2



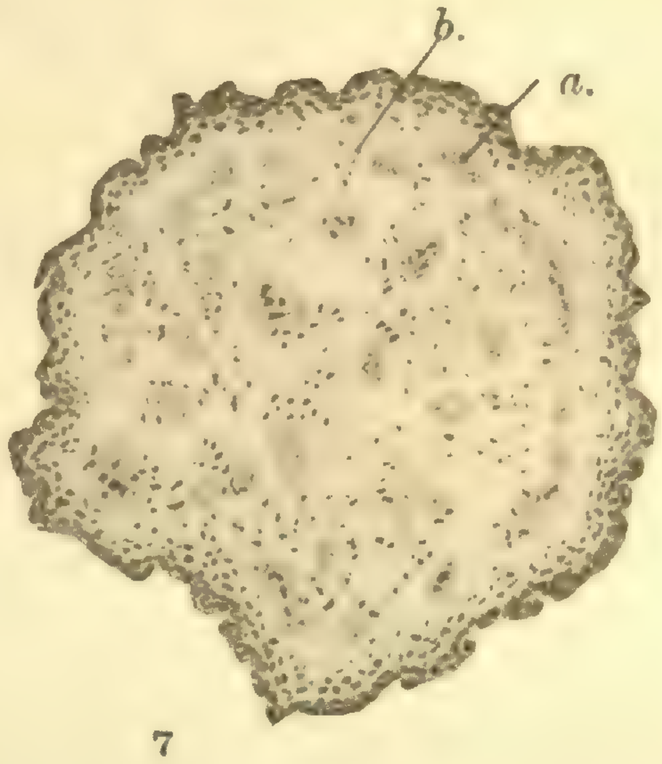
8

3



6

4



7

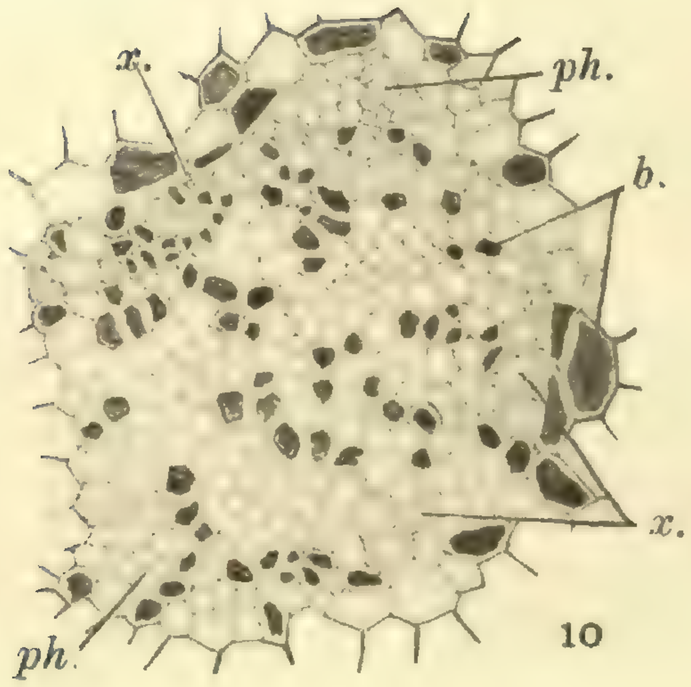
5

R.J.H-G. del.

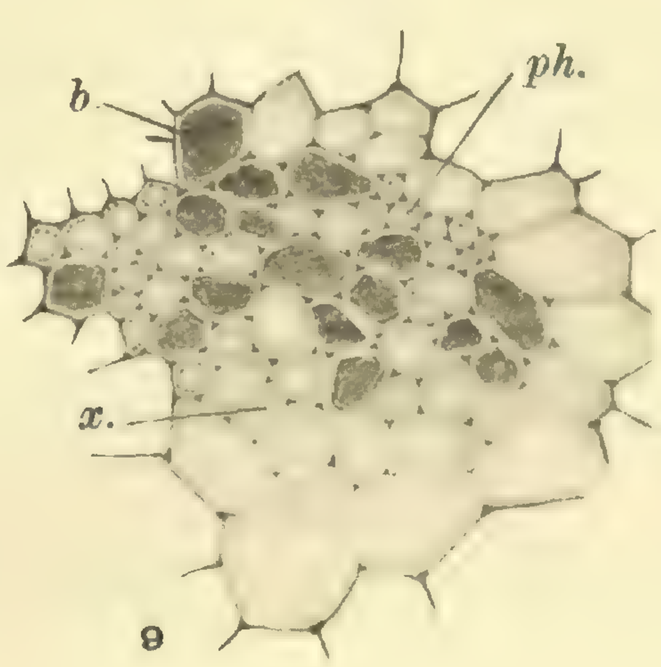
MYSTROPETALON, HARV.

11

15



10

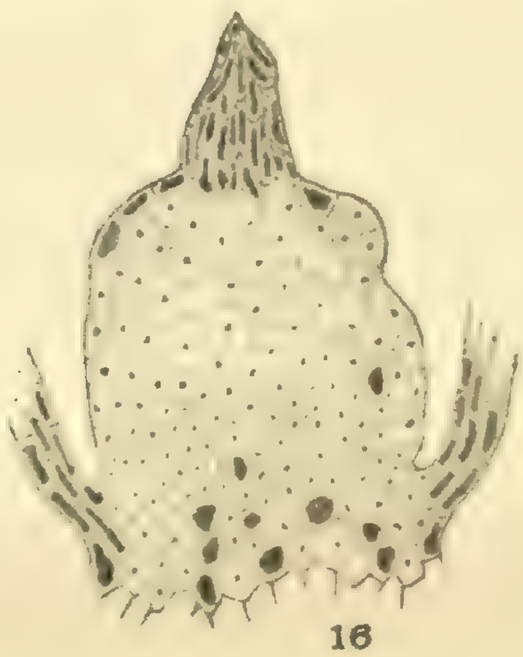


9

12

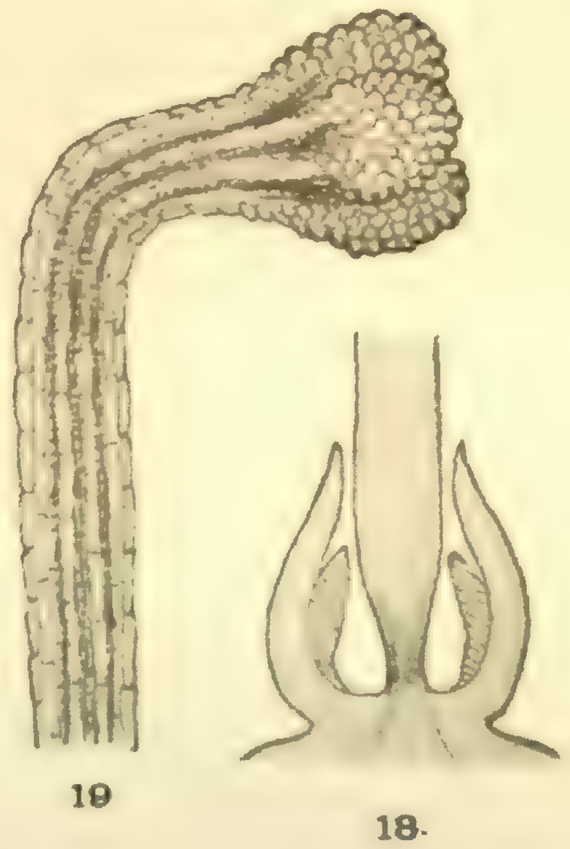
13

14

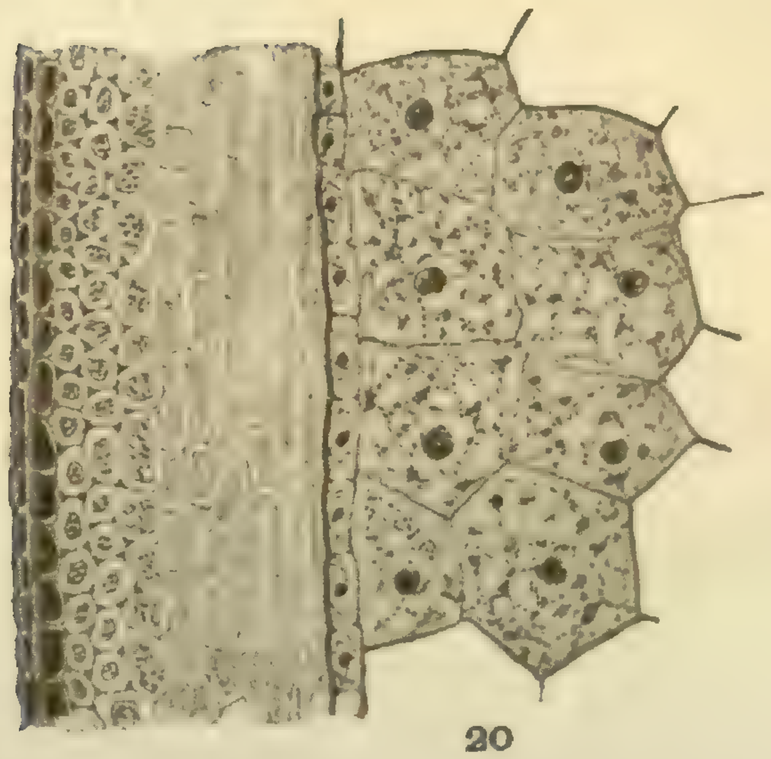

16

17

21


19

18.


20

R.J.H-G. del.

MYSTROPETALON, Harv.

London Lithographic Co. imp.

LINNEAN SOCIETY OF LONDON.

MEMORANDA CONCERNING TRANSACTIONS.

The First Series of the Transactions, containing both Botanical and Zoological contributions, has been completed in 30 Vols., and a few entire sets are still for sale. Only certain single volumes, or parts to complete sets, may be obtained at the original prices. The price of the Index to Vols. 1–25 is 8*s*. to the public, and 6*s*. to Fellows; to Vols. 26–30, 4*s*. to the public, and 3*s*. to Fellows.

The Second Series of the Transactions is divided into Zoological and Botanical sections. The prices of the Botanical parts of these which have been published are as undermentioned. (For the Zoological parts see Zoological wrapper.)

SECOND SERIES.—BOTANY.

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
I.	Parts I.–IX. (complete). 1875–80.	8	1	0	6	1	0
II.	Parts I.–XVI. (complete). 1881–88.	6	16	10	5	2	3
III.	Part I. 1888.	3	12	0	2	14	0
	Part II. 1891.	0	5	0	0	3	9
	Part III. 1891.	0	7	0	0	5	3
	Part IV. 1891.	0	6	0	0	4	6
	Part V. 1891.	0	6	0	0	4	6
	Part VI. 1891.	0	3	6	0	2	8
	Part VII. 1892.	0	6	0	0	4	6
	Part VIII. 1893.	0	6	0	0	4	6
	Part IX. 1893.	1	8	0	1	1	0
	Part X. 1894.	0	10	0	0	7	6
	Part XI. 1894.	0	3	4	0	2	6
IV.	Part I. 1894.	1	0	0	0	15	0
	Part II. 1894.	2	0	0	1	10	0
	Part III. 1895.	2	10	0	1	17	0
	Part IV. 1895.	0	3	4	0	2	6
V.	Part I. 1895.	0	9	0	0	6	9
	Part II. 1895.	0	12	0	0	9	0
	Part III. 1896.	0	6	0	0	4	6
	Part IV. 1896.	1	0	0	0	15	0
	Part V. 1896.	0	14	0	0	10	6
	Part VI. 1896.	0	4	0	0	3	0
	Part VII. 1897.	0	4	0	0	3	0
	Part VIII. 1897.	0	6	0	0	4	6
	Part IX. 1899.	0	12	0	0	9	0
	Part X. 1899.	0	6	0	0	4	6
	Part XI. 1899.	0	7	0	0	5	3
	Part XII. 1899.	0	12	0	0	9	0
	Part XIII. 1900.	0	1	6	0	1	2
	Part XIV. 1900.	0	3	0	0	2	3
	Part XV. 1901.	0	6	0	0	4	6

SECOND SERIES.—BOTANY (*continued*).

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
VI.	Part I. 1901.	1	10	0	1	2	6
	Part II. 1901.	0	6	0	0	4	6
	Part III. 1902.	0	18	0	0	13	6
	Part IV. 1903.	0	8	0	0	6	0
	Part V. 1903.	0	8	0	0	6	0
	Part VI. 1903.	0	12	0	0	9	0
	Part VII. 1904.	0	12	0	0	9	0
	Part VIII. 1904.	0	12	0	0	9	0
	Part IX. 1904.	0	7	0	0	5	3
	Part X. 1904.	0	14	0	0	10	6
	Part XI. 1905.	0	4	0	0	3	0
VII.	Part I. 1904.	0	5	0	0	3	9
	Part II. 1905.	0	6	0	0	4	6
	Part III. 1906.	0	3	0	0	2	3
	Part IV. 1906.	0	7	0	0	5	3
	Part V. 1907.	0	10	0	0	7	6
	Part VI. 1907.	0	4	0	0	3	0
	Part VII. 1907.	0	6	0	0	4	6
	Part VIII. 1908.	0	5	0	0	3	9
	Part IX. 1908.	0	2	6	0	2	0
	Part X. 1908.	0	7	0	0	5	3
	Part XI. 1909.	0	4	0	0	3	0
	Part XII. 1909.	0	12	0	0	9	0
	Part XIII. 1909.	0	5	0	0	3	9
	Part XIV. 1909.	0	6	0	0	4	6
	Part XV. 1910.	0	6	0	0	4	6
	Part XVI. 1912.	0	3	0	0	2	3
	Part XVII. 1912.	0	8	0	0	6	0
	Part XVIII. 1912.	0	5	0	0	3	9
	Part XIX. 1912.	0	3	0	0	2	3
	Part XX. Index.	0	3	0	0	2	3
VIII.	Part I. 1913.	1	0	0	0	15	0
	Part II. 1913.	0	8	0	0	6	0
	Part III. 1913.	0	8	0	0	6	0
	Part IV. 1913.	0	4	0	0	3	0

2nd Ser. BOTANY.] [VOL. VIII. PART 5.

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

ON THE CUTICLES OF SOME RECENT AND FOSSIL CYCADEAN FRONDS.

BY

H. HAMSHAW THOMAS, M.A., F.G.S.,

CURATOR OF THE BOTANICAL MUSEUM, CAMBRIDGE,

AND

NELLIE BANCROFT, B.Sc., F.L.S.,

1851 RESEARCH SCHOLAR, NEWNHAM COLLEGE, CAMBRIDGE.

LONDON:

PRINTED FOR THE LINNEAN SOCIETY

BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON-HOUSE, PICCADILLY, W.,

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

December 1913.

ERRATA.

Transactions of the Linnean Society, Ser. 2, Botany, Vol. VIII. Part 5.

Page

179, line 17 should read "PTILOPHYLLUM PECTEN (Phill.) Morris."

182 „ 5, for *Stangeria* read *Ptilophyllum*.

186 „ 1 should read "OTOZAMITES GRAPHICUS (Leck.) Schimp."

187 „ 17 „ "ANOMOZAMITES NILSSONI (Phill.) Sew."

190 „ 24 „ "NILSSONIA COMPTA (Phill.) Bronn."

191 „ 4 from bottom should read "NILSSONIA MEDIANA (Leck.) Fox-Strangw."

194 „ 7 should read "PTILOZAMITES LECKENBYI (Leck.) Nath."

VI. *On the Cuticles of some Recent and Fossil Cycadean Fronds.*

By H. Hamshaw Thomas, *M.A., F.G.S., Curator of the Botanical Museum, Cambridge, and* Nellie Bancroft, *B.Sc., F.L.S.*, 1851 *Research Scholar, Newnham College, Cambridge.*

(Plates 17–20. and 32 Text-figures.)

Read 6th November, 1913.

Contents.

	Page
I. Introduction	155
II. Cuticles of some Recent Cycads	157
(*a.*) Material and Methods	157
(*b.*) Previous references	157
(*c.*) Description of the Cuticles	158
i. Introduction	158
ii. Detailed description	158
iii. General summary of the structure of the recent Cuticles	174
III. Cuticles of Fossil Cycadean Fronds	177
(*a.*) Previous observations on cuticular structure	177
(*b.*) Detailed description	179
(*c.*) The Cuticles of some other types of Fossil Cycadean fronds	194
(*d.*) Summary of the structure of the Fossil Cuticles	195
IV. Comparison of the Cuticular Structure of Recent and Fossil Cycadean Fronds, with notes on that of other Gymnosperms	197

I. INTRODUCTION.

In an investigation of the cuticles of recent and fossil Cycads our attention is principally concentrated on the form and structure of the stomata, a study of which has attracted many observers. The physiological functions of the guard-cells are so important, and their shape and action are so uniform in plants of widely separated classes, that they may be regarded as highly adapted to their special work, and as structures which were evolved at a comparatively early period in phylogenetic development. But while the morphology of the stomata is uniform, many differences of structure, especially of thickening, do exist, rendering the work of classifying stomata by no means easy. One of the few general attempts to make a survey of the whole range of these structures, to classify them in groups, and to find broad general tendencies in their variation, is that of Porsch (1905), who has introduced a conception of a phylogenetic ground-plan modified by adaptations to external conditions. The idea that stomatal structures

may be valuable from the phylogenetic standpoint has not yet been worked out in any detail, nor has any attempt been made to compare modern plants with their fossil ancestors with regard to this character. One of us (Thomas, 1911) has shown, however, that some of the Carboniferous Calamites possessed the transverse bands of thickening which are so characteristic of the guard-cells of the modern Equisetums, and it seemed important to make further investigations of this kind. An especially favourable opportunity is presented in the Cycadophyta; the modern representatives of this group possess considerable variety of frond form, while the fossil fronds are also varied, and are abundant in a fairly good state of preservation in Mesozoic rocks. From a purely palæobotanical standpoint the work offers some attractions, because we have so often to deal with isolated fossil fronds which possess few points of distinction apart from external form; the possibility of classifying them and obtaining information as to their affinities by means of a study of their epidermal structure seems important.

So long ago as 1856 Bornemann made a brief comparative study of the epidermal characters of recent Cycads for the purpose of identifying fragments of fossil Cycadean fronds from the Lettenkohle beds of Thuringia, but his studies of the fossil forms were not very critical. He thought that the Mesozoic fronds were nearly related to if not generically identical with, some of the modern forms, and therefore expected that the study of the latter would at once facilitate the identification of the fossils. We are now tending to regard the fossil Cycads as more and more widely separated from their recent representatives, and we may at the outset expect the similarities in their structure to be few.

Recent work on the fossil and living members of the Cycadophyta has raised them to a very important position among the Gymnosperms. The investigation of the Carboniferous Pteridosperms, and the recent discoveries with regard to the Bennettitales have caused many botanists to seek for the origin of the Angiosperms amongst the ancestral plexus of Cycadean forms, much attention having been focussed on the Mesozoic plants of this affinity. It is, therefore, important to utilise every form of evidence as to the relationships of these plants.

The method of enquiry adopted in the present paper is, first, the detailed investigation of the epidermal structures found in the modern Cycads, and the attempt to find a type of stomatal structure characteristic of the group, the departures in detail from this type being noted. Subsequently, the epidermal structures of all the available Mesozoic fronds are described, and an attempt is made to estimate their relations in this respect to one another and to the modern fronds. In studying the fossil fronds, although we have many beautifully preserved examples of their cuticles, yielding much information in surface view, we have as yet been unable to get satisfactory preparations showing the guard-cells of the stomata in section; we are thus placed in an unfavourable position for comparing them with the recent structures.

II. CUTICLES OF SOME RECENT CYCADS.

(*a.*) Material and Methods.—Most of the material used in the investigation of recent cuticles was specially obtained from the Glasnevin Botanical Gardens, Dublin, and from Kew, and was fixed in medium chromacetic acid. In some cases ordinary laboratory material was used.

The types examined included *Cycas* (5 species), *Dioon* (2), *Ceratozamia* (3), *Macrozamia* (6), *Zamia* (8), *Encephalartos* (8), *Bowenia* (1 form), *Stangeria* (2 forms), *Microcycas* being the only genus unrepresented.

The upper and lower cuticles of the leaves were examined in surface view and in section. In many cases the epidermises were stripped off easily, but in others it was necessary to use Schulze's macerating fluid. Sometimes pinnæ were treated with the fluid and then washed in ammonia, as in the case of the fossil cuticles (*vide infra*); after this treatment only the cutin layer remains, with little or no trace of underlying cells.

Permanent preparations of cuticles removed in either of the above ways were made. Bismarck brown, Congo red, and diamant fuchsin were used for staining. Lloyd (1908), in his researches on the Physiology of Stomata, seems to consider Congo red more satisfactory as an epidermal stain than Bismarck brown; in the present case diamant fuchsin was most used, as it is very rapid. The stain fades a little, however, on exposure of the preparations. Unstained preparations of cuticles were also largely used. In the case of the sections, one of the most satisfactory stains was found to be Scharlach R (also used for macerated cuticles) prepared as directed by Hill (1912). By it the cutin layer and cuticularised parts were clearly defined, staining a bright brownish red, all the other tissues remaining unaffected. Phloroglucin with hydrochloric acid was used to show the lignified lamellæ which occur in every case on the dorsal and ventral walls of the guard-cells. Serial sections stained with cotton red and aniline blue, and with diamant fuchsin were employed in the correlation of surface views and sections of stomata. Other tests were used, but an account of them need not be repeated here, as descriptions are to be found in the literature quoted.

(*b.*) Previous References.—The most important previous accounts of the epidermises of Cycads include that given by Bornemann (1856), whose description is in connection with some fossil types and includes remarks on the chemistry of the epidermal walls and on the preparation of "artificial cuticles"; Kraus (1866) and Nestler (1895) also give good descriptions of some Cycadean cuticles. These researches show that each genus is fairly well characterised by a peculiar epidermis; sometimes the genera may be divided into sub-groups according to the structure of the epidermis (see Bornemann, 1856, p. 42, and Kraus, 1866, p. 13). Figures and descriptions of the stomata of some Cycads are given by Schwendener (1881), Strasburger (1866–67), Mahlert (1885), and Porsch (1905). More detailed references will be given in the description of each genus. The last-named author mentions the fact that though there is a general type of stoma characteristic of the Gymnosperms as a whole, there is one special type for almost each genus when the finer structure is taken into consideration.

(*c.*) Description of the Cuticles.

(i.) Introduction.

In a consideration of the cuticles * of recent Cycads with a view to comparing them with those of fossil fronds, the features which seem to be of greatest value are those which may be determined from an examination of surface views. The actual form, size, and arrangement of the guard-cells, and the thickening of their walls as seen in section, are very constant throughout the group, and the variations mostly depend upon the appearance in surface view. The chief features to be taken into consideration are as follows :—

(1) The form and outline of the epidermal cells of upper and lower surfaces of the leaves, both between and over the nerve-courses ; the pitting and thickness, straightness or irregularity of the cell-walls.

(2) The distribution and position of the stomata, whether scattered or in definite restricted areas; whether irregularly placed or having their axes in a fixed direction with regard to the axis of the pinna.

(3) The appearance of the stomata in surface view, depending upon the presence or absence of an intercalated series of cells between the guard-cells and the general epidermal cells, and the consequent degree of sinking of the guard-cells below the epidermis ; the shape of the stoma-opening.

(4) The number and arrangement of the subsidiary cells † (the epidermal cells surrounding the stoma, or in the case of much sunk guard-cells, those around the stoma-opening at the surface of the leaf).

(5) The presence or absence of crystals, either in the epidermal cells or in intercellular spaces.

(6) The presence or absence of hairs or hair-scars.

(7) The thickness of the cutin layer, and the presence or absence of foldings or striations upon it.

(ii.) Detailed Description.

Stangeria, T. Moore. Pl. 17. figs. 1–6 ; text-fig. 1.

References :—Bornemann (1856), pp. 41, 45 ; Taf. 12. figs. 19, 20. Kraus (1866), p. 34 ; Taf. 23. figs. 28, 29. Nestler (1895), p. 363.

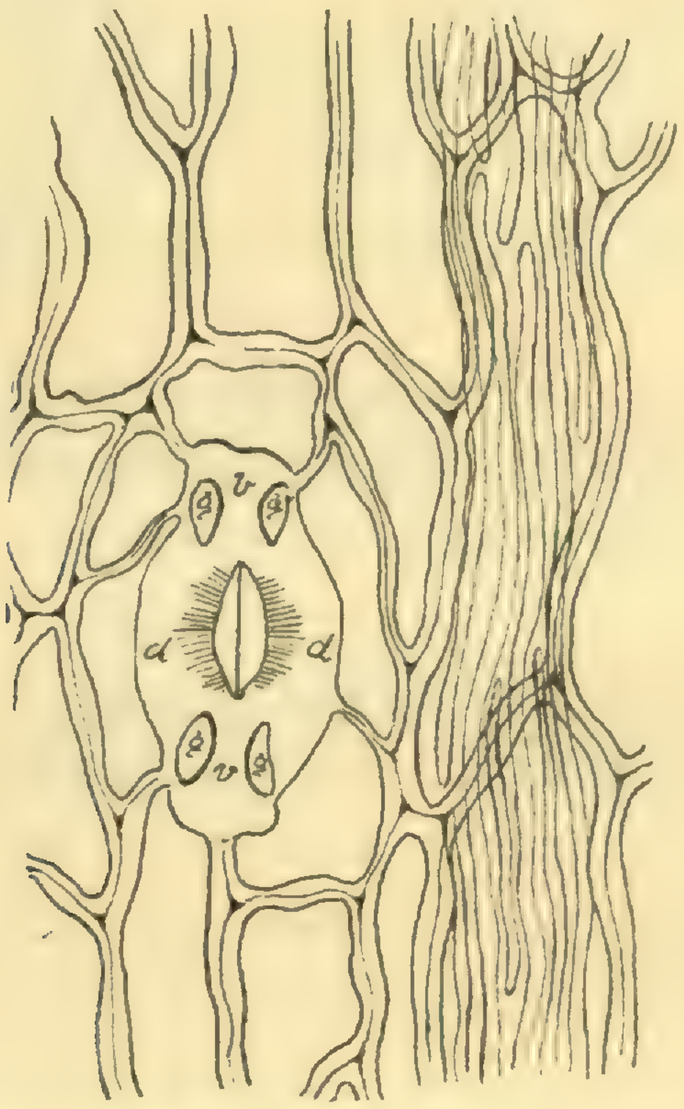
The typical *Stangeria paradoxa*, T. Moore, and its variety *schizodon*, were examined and found to be exactly similar in epidermal and cuticular characters. The genus is distinct from all other Cycads, in that the epidermal cells of both upper and lower surfaces of the leaf-lamina have undulate lateral walls, like those of the epidermal cells of ferns. These cells are irregular in form and arrangement, and are usually three- or four-angular. Over the midrib of the pinnæ the undulations are absent, and the cells

* The term "cuticles" is used to include the layer of epidermal cells and the overlying layer of cutin.

† "Wall-Zellen" or "Nebenzellen" of the German authors.

are more regularly rectangular (text-fig. 1). Over the lateral veins also the cells are somewhat rectangular, narrow, and elongated, but the walls are undulate. At the pinna-margins the cells gradually become smaller and straight-walled. According to Kraus the cell-walls are unequally thickened, more secondary material being laid down on the outer side of a bend than the inner. Very little difference was noted in the present case, perhaps owing to the comparative thinness of the walls; and after careful preparation and staining, it seemed as if the slight inequality might be due to optical effect rather than to any real difference in the amount of thickening.

Fig. 1.



Stangeria paradoxa: surface view of the cuticle from the midrib of the upper side of the leaf, showing a stoma with characteristic thickening due to the dorsal (*d*) and ventral (*v*) lignified lamellæ of the guard-cells; *g*, the raised polar ends of the guard-cells. Note the absence of folds of the cutin in the neighbourhood of the stoma. × 450.

Stomata occur scattered and irregularly-placed with regard to the pinna-axis, on the lower side of the lamina; they are generally absent in the very narrow areas over the lateral veins. They occur on both upper and lower mid-rib areas, their long axis being parallel with that of the pinna (text-fig. 1). The upper, as well as the lower stomata appear to be functional, as there is a well-developed air-space underlying each.

The stomata lie practically at the level of the epidermis (Pl. 17. figs. 1 & 5); the guard-cells are not sunk as in the case of *Zamia* (*cf.* Pl. 17. fig. 5 with Pl. 18. fig. 13). Each stoma is surrounded by from four to six epidermal cells having slightly thinner. straighter walls than the rest of the epidermis. These "subsidiary cells" are particularly marked in the case of the lower stomata, and may usually be distinguished into polar and lateral cells; Pl. 17. fig. 1 shows an example with two polar and two lateral subsidiary cells. Division of the lateral cells often takes place, as text-fig. 1 shows.

The cavities of the subsidiary cells in many cases contain crystals of calcium oxalate *. The stomata are elliptical in shape, and in surface view the lignified lamellæ † of the ventral and dorsal walls of the guard-cells give a very characteristic thickened appearance (Pl. 17. fig. 1; text-fig. 1) to the area overlying the guard-cells. This thickened area surrounding the pore of the stoma shows two thin patches at each pole, owing to the raising up of the polar ends of the guard-cells, bringing them nearer to the surface at these points, as described by Porsch for *Bowenia*. The projections of thickening substance between each pair of thin areas strengthening the ends of the stoma-opening are due to the extension of the ventral lignified lamellæ of the guard-cells (see text-fig. 26, p. 176). Laterally the cutin overlying the lamellæ shows fine striations (Pl. 17. fig. 1; text-fig. 1).

Hair-scars occur on the lower surface of the pinnæ, particularly on and near the midrib and at the margins. They are only to be seen here and there on the upper midrib. The scars are somewhat like a truncated cone in shape and are strongly cuticularised (Pl. 17. figs. 2 & 6).

The cutin layer overlying the epidermal cells is fairly thick, particularly on the upper surface of the pinnæ. It has closely-lying striations which are seen from sections to be due to folds (Pl. 17. fig. 3). These folds are particularly marked on the upper surface, and are irregular on the lamina, but are regular and run in a longitudinal direction on the midrib (text-fig. 1). They radiate from the poles of the stomata and from the bases of the hair-scars (Pl. 17. figs. 1 & 2; see also references quoted). Folding of the cutin is not to be found in any other genus of Cycads, and constitutes, with the undulate epidermal walls, a distinguishing feature of *Stangeria*.

Cycas, Linn. Pl. 17. figs. 10–15; text-figs. 2 & 3.

References:—Bornemann (1856), pp. 40, 42; Taf. 11. figs. 3–6. Kraus (1866), p. 31; Taf. 19. figs. 1–6; Taf. 20. figs. 10, 11. Strasburger (1866), Taf. 41. fig. 143. Mahlert (1885), Taf. 1. fig. 20. Nestler (1895), p. 343.

Species examined:—*C. revoluta*, Thunb.; *C. circinalis*, Linn.; *C. undulata*, Desf.; *C. Micholitzii*, Dyer; *C. media*, R. Br.

The epidermal cells of *Cycas* are similar on both sides of the pinnæ, and are more or less irregular in shape and arrangement. They are usually somewhat elongated, and are three- to six-angular. Over the midrib the cells are more regular and rectangular in shape and run parallel with the pinna-axis. In these points there is general agreement with *Stangeria*. In *Cycas*, however, the lateral epidermal walls are not undulate, being at the most somewhat curved. A distinguishing feature of all species of *Cycas* examined ‡ is the pitting of the outer walls of the epidermal cells (Pl. 17. figs. 10–13, fig. 15; text-fig. 2). In surface view and sections, these walls are seen to be perforated

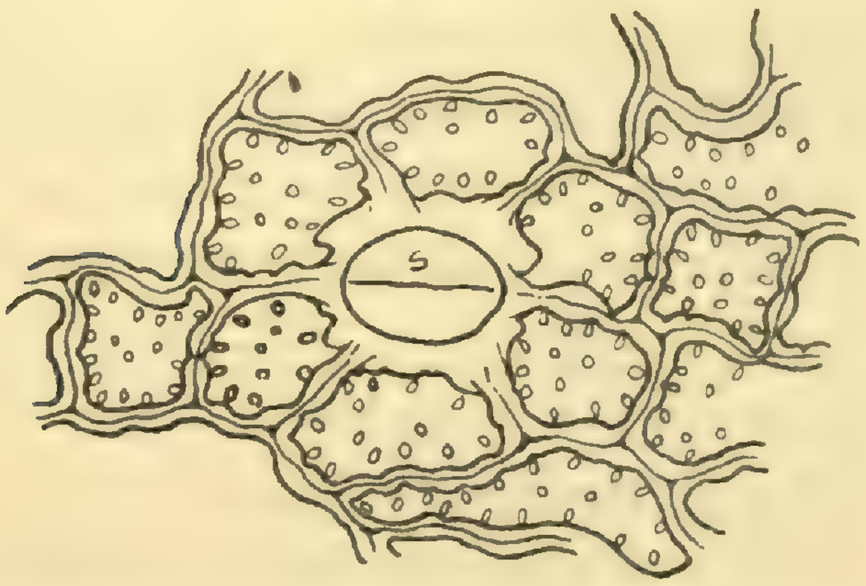
* *Cf.* Kraus (1866), Pl. 23. fig. 29; the example figured in Pl. 17. fig. 1, does not show these crystals, owing to previous maceration.

† Porsch (1905); see also Karzel (1907).

‡ See also the lists given by Bornemann and Kraus.

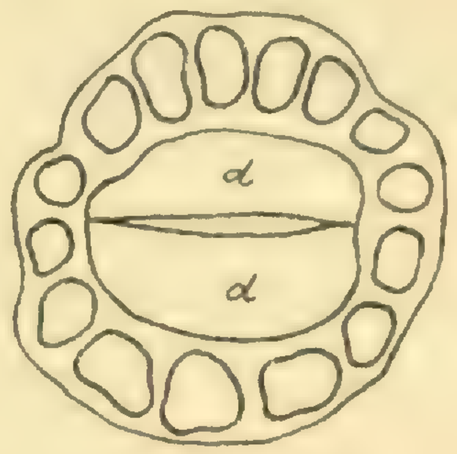
by more or less regularly-disposed pores, which occur principally towards the periphery of the cells and which are covered by the cutin layer. This pitting occurs in both the upper and lower epidermis, and is not known to be present in any other genus of the Cycadaceæ *. The pores vary considerably in size in the different species of *Cycas*: the largest were observed in *C. circinalis*, the smallest in *C. Micholitzii*. Pitting of the lateral walls also occurs, but in a varying degree (Pl. 17. figs. 10 & 13). It is well marked in *C. revoluta* ; in *C. undulata*, however, pits occur only here and there.

Fig. 2.



Cycas Micholitzii.—Lower cuticle in surface view: *s*, a stoma-opening, surrounded by six subsidiary cells. The thickened appearance round the stoma-opening is due to the showing-through of the cutin layer lining the air-space and overlying the guard-cells. × 450.

Fig. 3.



Cycas revoluta.—A stoma in surface view, focussed below the level shown in Pl. 17. fig. 12, so that the dorsal or upper surfaces (*d*) of the guard-cells are seen surrounded by fifteen small cells, the intercalated series shown in section in Pl. 17. fig. 13. × 450.

Stomata occur only on the underside of the pinnæ, and are scattered and irregular in position. As both Bornemann and Kraus have previously mentioned, the species of *Cycas* fall into two groups, according to their epidermal and stomatal characters, which, moreover, correspond with the external characters of the leaves. The first group contains species such as *C. revoluta*, with narrow pinnæ, the margins of which are inrolled †; the second group, of which *C. circinalis* is an example, contains species with broader, flatter pinnæ, less xerophytic in texture than those of the first group. All the types examined, with the exception of *C. revoluta*, belong to this group.

In the first type the epidermal cells are irregular in shape and disposition, particularly on the under side of the pinnæ, where, however, they are more isodiametric; their greatest diameter often lies transversely to the pinna-axis. The most distinctive feature of the cuticle consists in the complication of the stomatal apparatus. The guard-cells are well sunk below the surface, and between them and the subsidiary cells, which in this case overarch the guard-cells and form an "outer air-space," is an intercalated series consisting of from twelve to fifteen small cells (Pl. 17. fig. 13; text-fig. 3‡). These

* *Microcycas* has not yet been examined.

† Bornemann and Kraus have also examined *C. inermis* in this group.

‡ *Cf.* Kraus (1866), Taf. 19. figs. 4 & 5.

intercalated cells appear to be derived from the same mother-cells as the subsidiary cells, which are also from twelve to fifteen in number. The subsidiary cells are narrowly and obliquely elongated (Pl. 17. fig. 13), so that they arch over the depression containing the guard-cells in such a way as to give the appearance, in surface view, of a somewhat hemispherical elevation, perforated by a small rounded opening (Pl. 17. fig. 12)*. The intercalated cells and subsidiary cells are pitted in the same way as the general epidermal cells (Pl. 17. fig. 13).

In the second group, the epidermal cells are irregular in form and position, as in the first type; the stomata, however, are more simple in organisation (Pl. 17. fig. 14). They are a little sunk below the general level of the epidermis, but there is no intercalated series and the subsidiary cells do not overarch the depression; hence the very different appearance of the stomata as seen in surface view (text-fig. 2). The subsidiary cells are fewer in number, though very variable, usually between five and nine (text-fig. 2); in shape they are from isodiametric to elliptical.

In *C. circinalis* and *C. revoluta*, fairly young stages were examined; these showed very distinctly the presence of hair-scars on the under surface of the leaves.

The cutin layer is in all species fairly thick; it is not characterised by any special foldings or markings, as in *Stangeria*.

ENCEPHALARTOS, Lehm. Pl. 18. figs. 10 & 11; text-figs. 4–8.

REFERENCES:—Bornemann (1856), pp. 40, 44; Taf. 13. figs. 1–6. Kraus (1866), pp. 33, 34; Taf. 20. figs. 12–15; Taf. 21. fig. 16. Mahlert (1885), Taf. 1. fig. 23. Nestler (1895), pp. 346–348; Taf. 11. figs. 5–8; Taf. 12. fig. 9.

SPECIES EXAMINED:—*E. villosus*, Lemaire; *E. Woodii* (? hort.); *E. horridus*, Lehm.; *E. caffer*, Miq.; *E. lanuginosus*, Lehm.; *E. Lehmanni*, Eckl.; *E. Ghellinckii*, Lem.; *E. Laurentianus*, Wilden. (See also the lists of Bornemann and Kraus.)

Reviewing the species examined as a whole, there seems to be a considerable amount of variation in the form of the epidermal cells, even in the cells of the same pinna (text-fig. 5). Generally speaking, the cells are somewhat elongated and the longitudinal axes run in the direction of the longitudinal axis of the pinna (Pl. 18. fig. 11; text-fig. 4). The transverse walls are usually obliquely placed with regard to the pinna-axis; the cells are three- or four-angular and rhombic in shape.

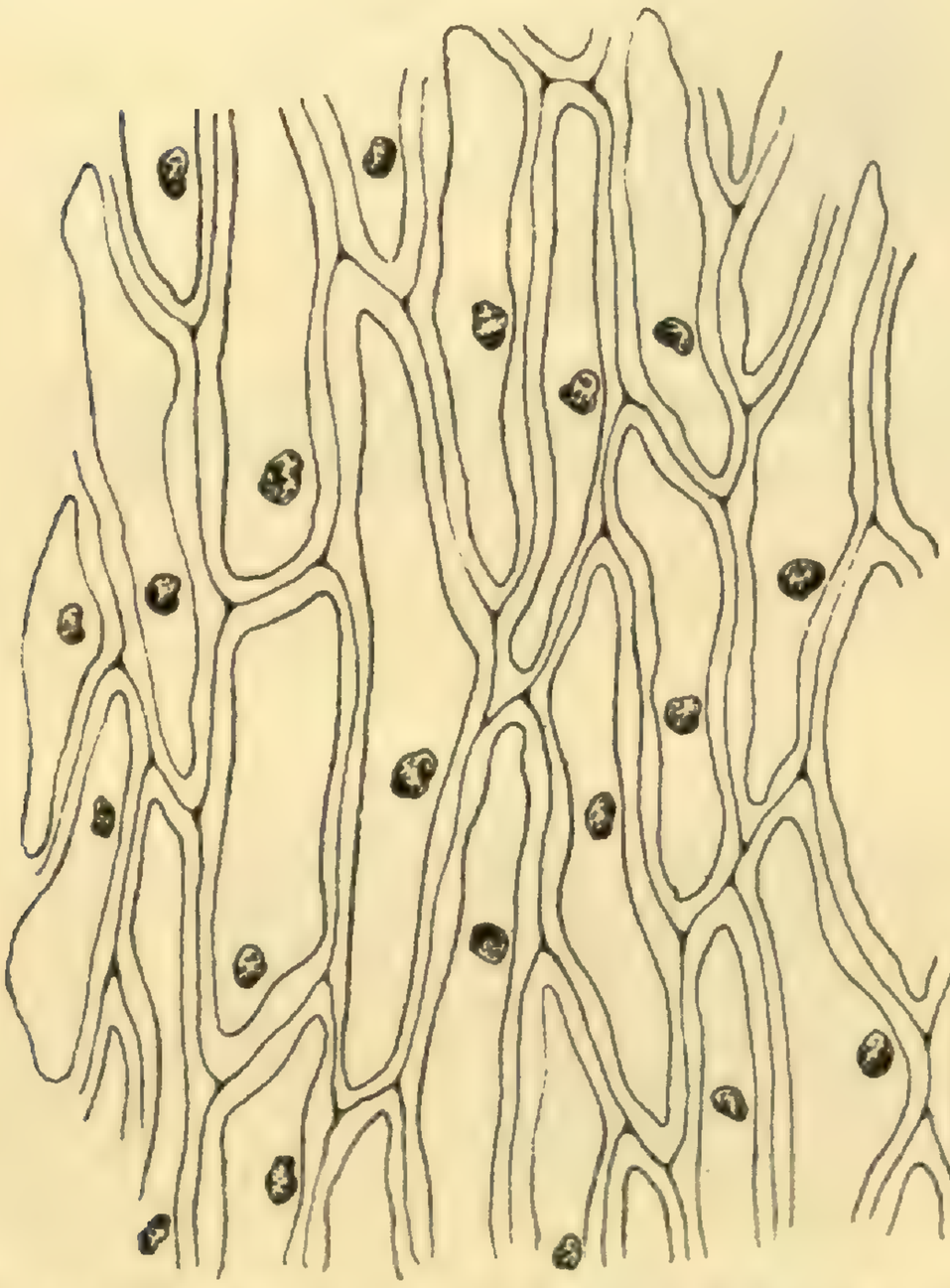
In *E. Lehmanni* (text-fig. 5), *E. caffer*, and *E. lanuginosus*, where the cells are small and more nearly isodiametric, their greater diameter is usually transversely or obliquely placed with regard to the axis of the pinnæ; in *E. horridus* the cells are irregular in form and direction, particularly in the region of the lobe-bases.

The epidermal cells of the lower surface are of two kinds—those of the nerve-courses and those of the stomatal areas. The cells of the nerve-courses are similar in form to those of the upper surface. They are usually somewhat narrow and elongated and are arranged in longitudinal lines. The cells of the stomatal areas are typically shorter, broader, and more isodiametric.

* *Cf.* Bornemann (1856), Taf. 11. fig. 4.

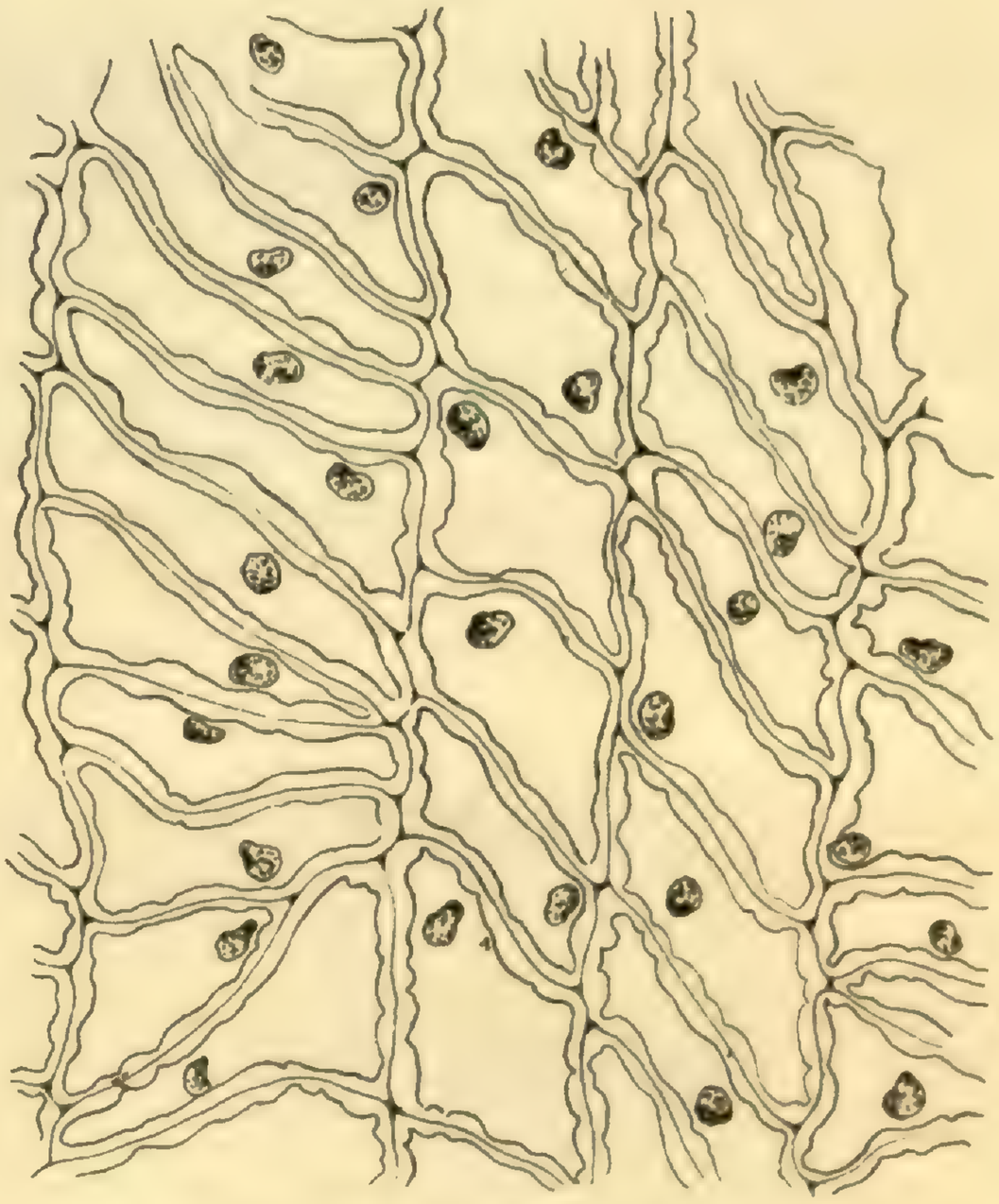
The walls of all the epidermal cells are without undulations, but are often slightly curved. In most of the cases examined, the lateral walls (*never* the outer walls) of both upper and lower epidermal cells are pitted in the same way as the lateral walls of *Cycas*. This is very marked in *E. Lehmanni* (Pl. 18. fig. 10; see also fig. 11). In *E. Woodii* and on the lower surface of *E. villosus* pittings are infrequent. In the examined species of *Encephalartos* the inner and lateral walls of the epidermal cells are often slightly

Fig. 4.



Encephalartos Woodii.—Upper cuticle in surface view, showing form and arrangement of epidermal cells. × 450.

Fig. 5.



E. Lehmanni.—Upper cuticle in surface view. × 450.

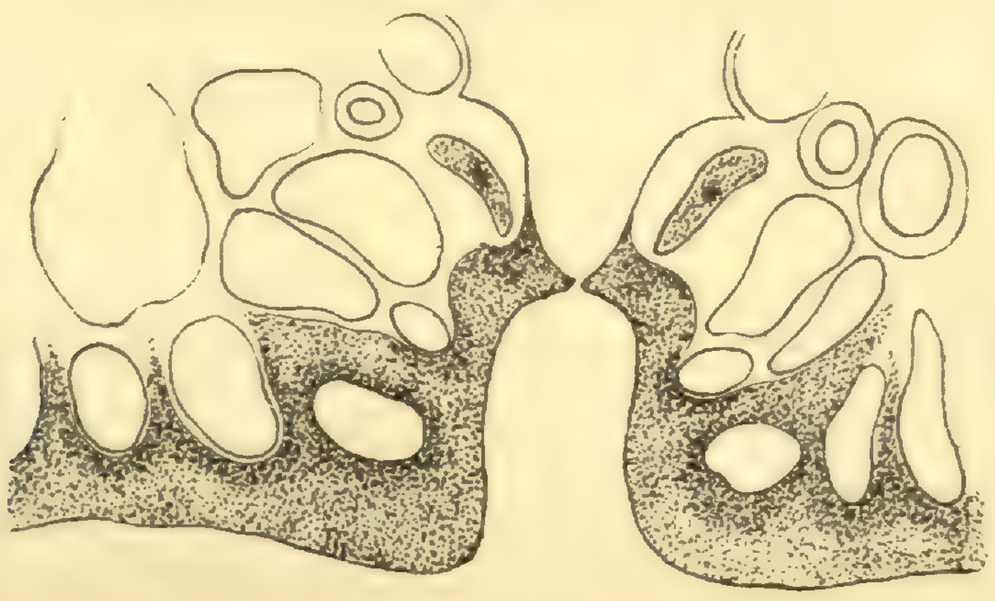
thicker than the outer walls (Pl. 18. fig. 10) Towards the pinna-margins the cells become smaller and thicker-walled. In some cases, as in *E. horridus* and *E. villosus* (Pl. 18. fig. 11), the elongated epidermal cells are septate.

Stomata are confined to the lower surface of the pinnæ, and more or less definitely to the areas between the nerve-courses. Their longitudinal axis is typically coincident with that of the pinna. They are in most cases considerably sunk below the general level of the epidermis without overarching of the subsidiary cells; so that the outer air-space is fairly long and narrow and tubular in shape (text-fig. 6). There is a somewhat irregular system of intercalated cells separating the guard-cells from the general epidermal cells. In median sections of the stomata, typically two intercalated cell-series appear (text-fig. 6); the sections may not, however, pass through a cell of both series. Nestler (1895, p. 348) mentions that one or two intercalated series are present; while according to Kraus (1866, p. 34) the guard-cells lie immediately under the epidermis except at the pinna-bases. The stoma-opening is somewhat elongated and elliptical to quadrangular in shape (text-

figs. 7 & 8). It is surrounded by from four to six subsidiary cells, and is strongly cuticularised.

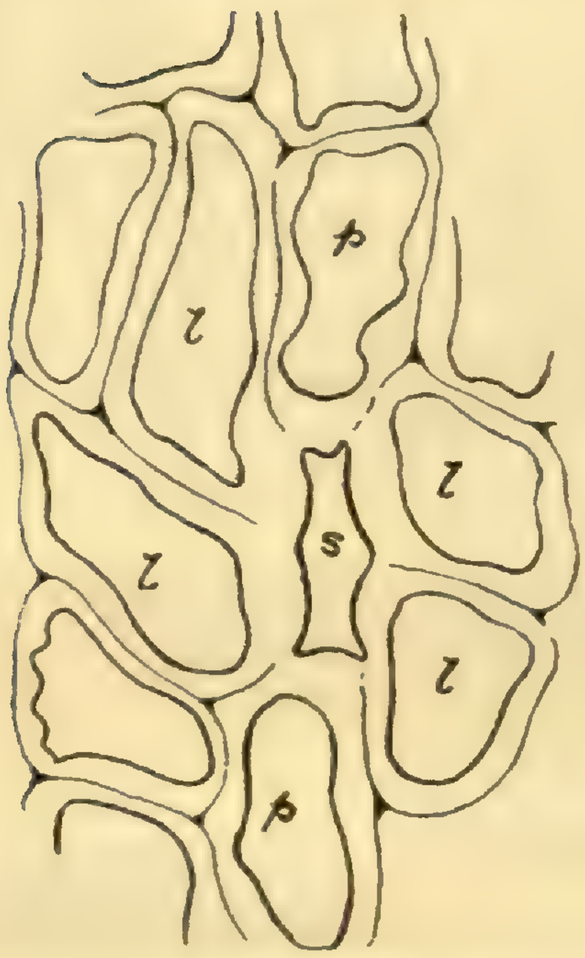
Simple hairs and hair-scars occur in *E. Ghellinckii*. In *E. caffer* crystals of calcium

Fig. 6.



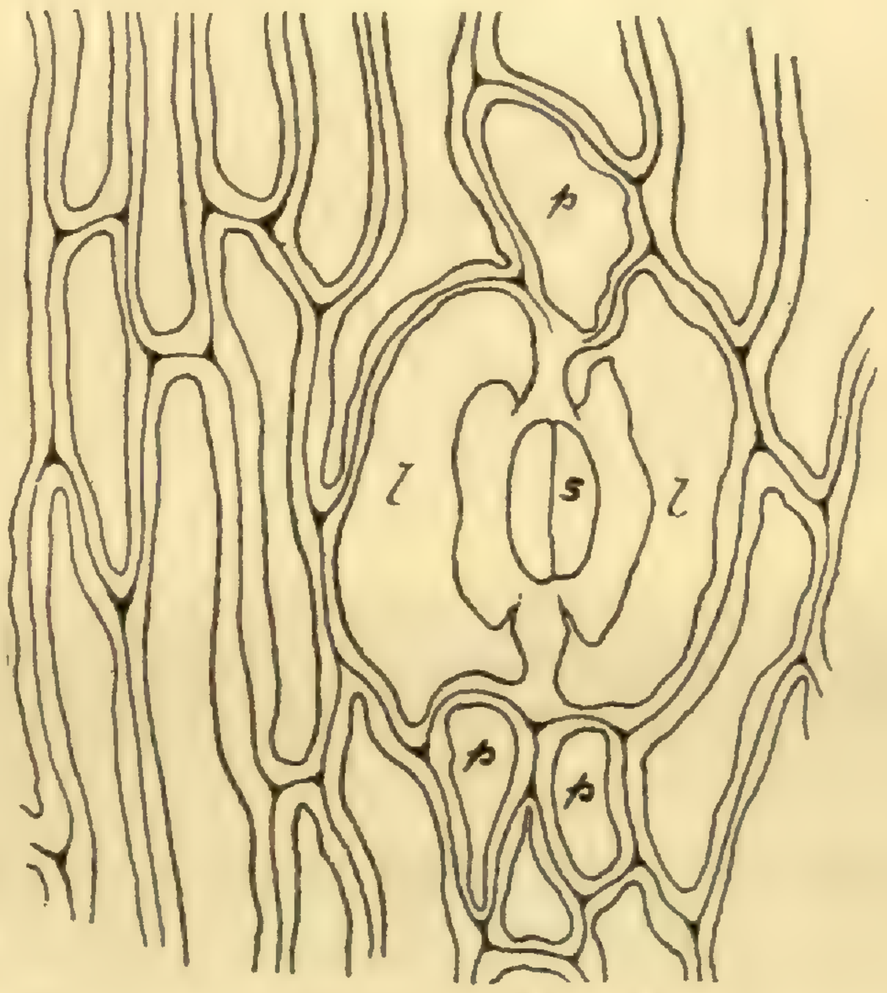
Encephalartos Lehmanni.—Section of the lower cuticle, showing a stoma in median section. Note the presence of intercalated cells between the guard-cells and subsidiary cells, and the heavy cuticularisation. × 450.

Fig. 7.



E. Lehmanni.—Lower cuticle (after maceration) in surface view, showing a stoma-opening (*s*) surrounded by six subsidiary cells (*p*, polar subsidiary cells; *l*, lateral subsidiary cells). × 450.

Fig. 8.



E. villosus.—Lower cuticle in surface view; the stoma-opening is surrounded by five subsidiary cells, one of the polar cells being divided. × 450. This cuticle was not removed by maceration, so that the thickening of the guard-cells and the lining of the outer air-space show through in the surface view, giving a much thickened appearance to the stoma-opening.

oxalate, such as figured by Nestler (1895, Taf. 11. figs. 6–8), were not observed; very little material of this species was, however, available.

The cutin layer is of a considerable thickness in the case of both upper and lower epidermises (Pl. 18. fig. 10; text-fig. 6).

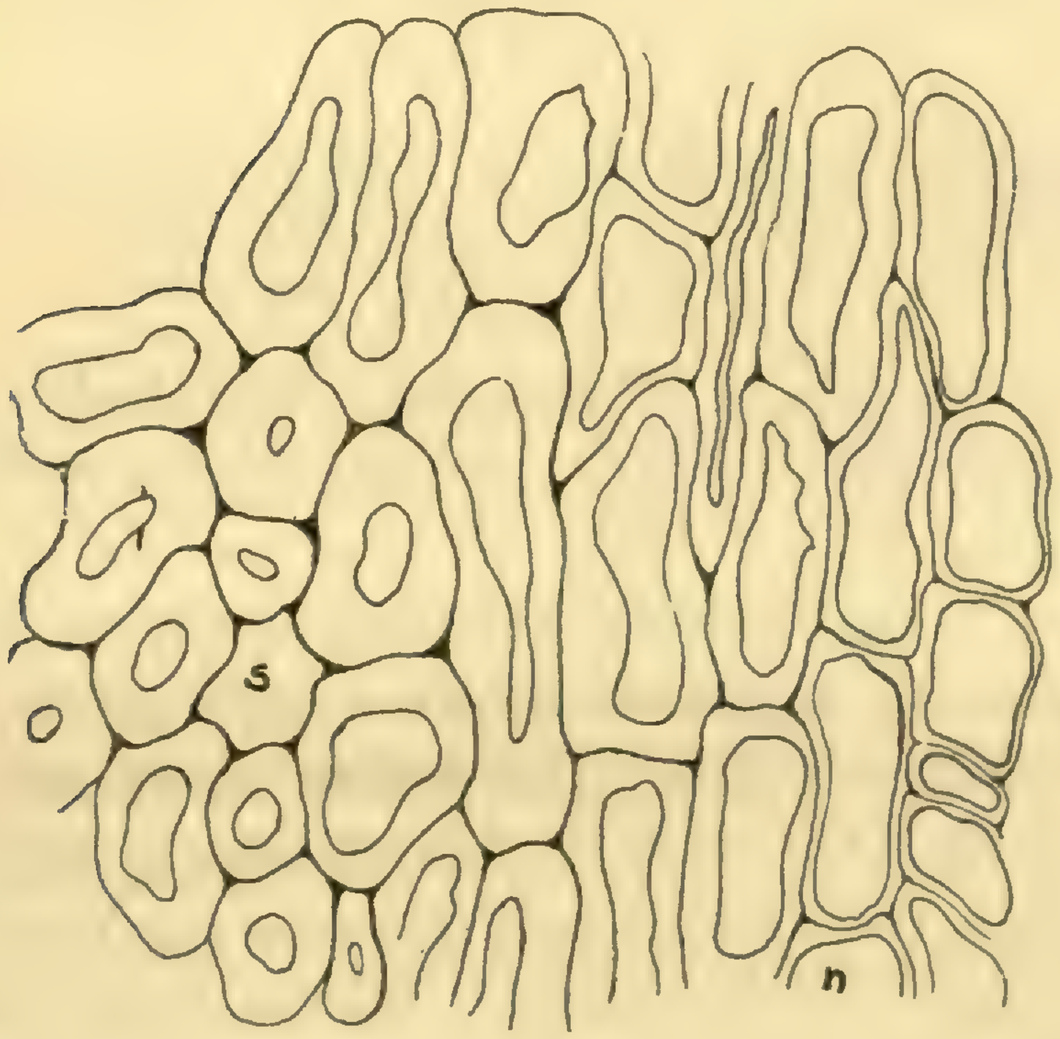
Dioon, Lindl. (Pl. 18. figs. 5–9; text-figs. 9 & 10.)

References :—Bornemann (1856), pp. 40, 45; Taf. 12. figs. 11–14. Kraus (1866), pp. 39, 40; Taf. 22. figs. 21–23. Mahlert (1885), Taf. 1. fig. 22. Porsch (1905), p. 11; Taf. 1. fig. 7.

Species examined :—*D. edule*, Lindl.; *D. spinulosum*, Dyer.

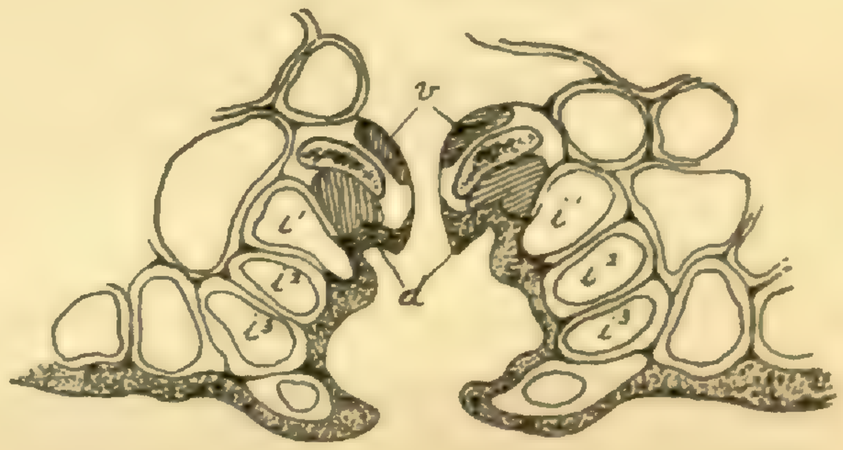
The two species were found to be of a similar type, characteristic for the genus. In *D. edule* the upper epidermal cells and those of the nerve-courses of the lower side of the pinnæ are similar, and are of two kinds—thick-walled cells elongated fairly regularly in the direction of the longitudinal pinna-axis, and more or less isodiametric thin-walled cells. These two kinds of cells may be distinguished in transverse section (Pl. 18. fig. 7). The thin-walled cells appear to be the more numerous. The cells of the stomatal regions between the nerve-courses are usually smaller than elsewhere. They are almost isodiametric and are uniformly thick-walled. In *D. spinulosum* the epidermal characters are similar to those in *D. edule*, though all the cell-walls seem to be slightly less thickened. In both cases the lateral walls of the cells are often slightly pitted (Pl. 18. fig. 5) (Kraus, 1866, fig. 21), and all the walls are more or less heavily layered

Fig. 9.



Dioon edule.—Lower cuticle in surface view, showing six subsidiary cells surrounding a stoma-opening, *s*. *Cf.* the epidermal cells of the nerve-course (*n*) with those of the upper surface shown in Pl. 18. fig. 5. × 450.

Fig. 10.



D. spinulosum.—A stoma in median section, showing the dorsal (*d*) and ventral (*v*) lignified lamellæ of the guard-cells, and three intercalated series of cells (i^1–i^3) between the guard-cells and subsidiary cells. (*Cf.* Pl. 18. fig. 6.) × 450.

(Pl. 18. figs. 5 & 9). In the case of the thick-walled cells of *D. edule*, the lumen is often almost filled up.

Stomata occur very definitely limited to the areas between the nerve-courses on the under surface of the leaves. They are much sunk in flask-shaped cavities, which are slightly deeper in *D. edule* than in *D. spinulosum*. In both species there are typically three intercalated series of cells between the guard and subsidiary cells (Pl. 18. fig. 6;

text-fig. 10) (Porsch, 1905, Taf. 1. fig. 7). The cavities are lined with a layer of cutin, and the epidermal cells surrounding the stoma-openings (subsidiary cells) arch over slightly. They are also a little raised beyond the surface of the pinna, and are rounded, as seen in surface view. They are from six to eight in number and are much thickened, especially in *D. edule* (text-fig. 9).

Crystals of calcium oxalate occur in *D. edule* on the lower side of the pinnæ in the nerve-courses. They were not observed on the upper side. Kraus figures a crystal from the lower epidermis, but does not specially note their occurrence there. He mentions that "here and there a thin-walled cell contains a crystal." So far as could be determined, however, from the appearance in surface view and in section, the crystals occur in cavities or spaces between the cells rather than in the cells themselves (Pl. 18. figs. 8 & 9); for in surface view the rounded ends of the neighbouring cells seem to project into a space, and in section Scharlach R shows the presence of a layer of cutin entirely surrounding or lining the crystal-containing space.* *D. spinulosum* has no crystals.

The cutin layer in both species is very thick, especially in *D. edule* (Pl. 18. figs. 7 & 8).

Ceratozamia, Brongn. Pl. 18. figs. 1–4; text-figs. 11 & 12.

References:—Bornemann (1856), pp. 40, 45; Taf. 12. figs. 7–10. Kraus (1886), pp. 38, 39; Taf. 21. figs. 17–20. Mahlert (1885), Taf. 1. fig. 21.

Species examined:—*C. mexicana*, Brongn.; *C. fusco-viridis*, D. Moore; *C. latifolia*, Miq.

These three species show the same general characters, all possessing two kinds of epidermal cells, thick- and thin-walled. The thick-walled cells apparently predominate in *Ceratozamia* (cf. *Dioon*), though they are somewhat variable in number and in distribution in the three species examined. There is considerable variation, moreover, in the relative thickness of the thick-walled cells; *C. mexicana* shows a very marked contrast between the two kinds of cells (Pl. 18. figs. 1 & 3); *C. latifolia* shows comparatively little difference between them (text-fig. 11); while *C. fusco-viridis* is intermediate in this respect. The cells—particularly the thicker-walled ones—are much elongated in the direction of the longitudinal axis of the pinna. The cells of the nerve-courses, in the lower epidermis, are similar to those of the upper side; while between the nerve-courses, as is usual, the cells are shorter and broader. Thin-walled cells occur in these areas also, especially in *C. mexicana* (cf. *Dioon*).

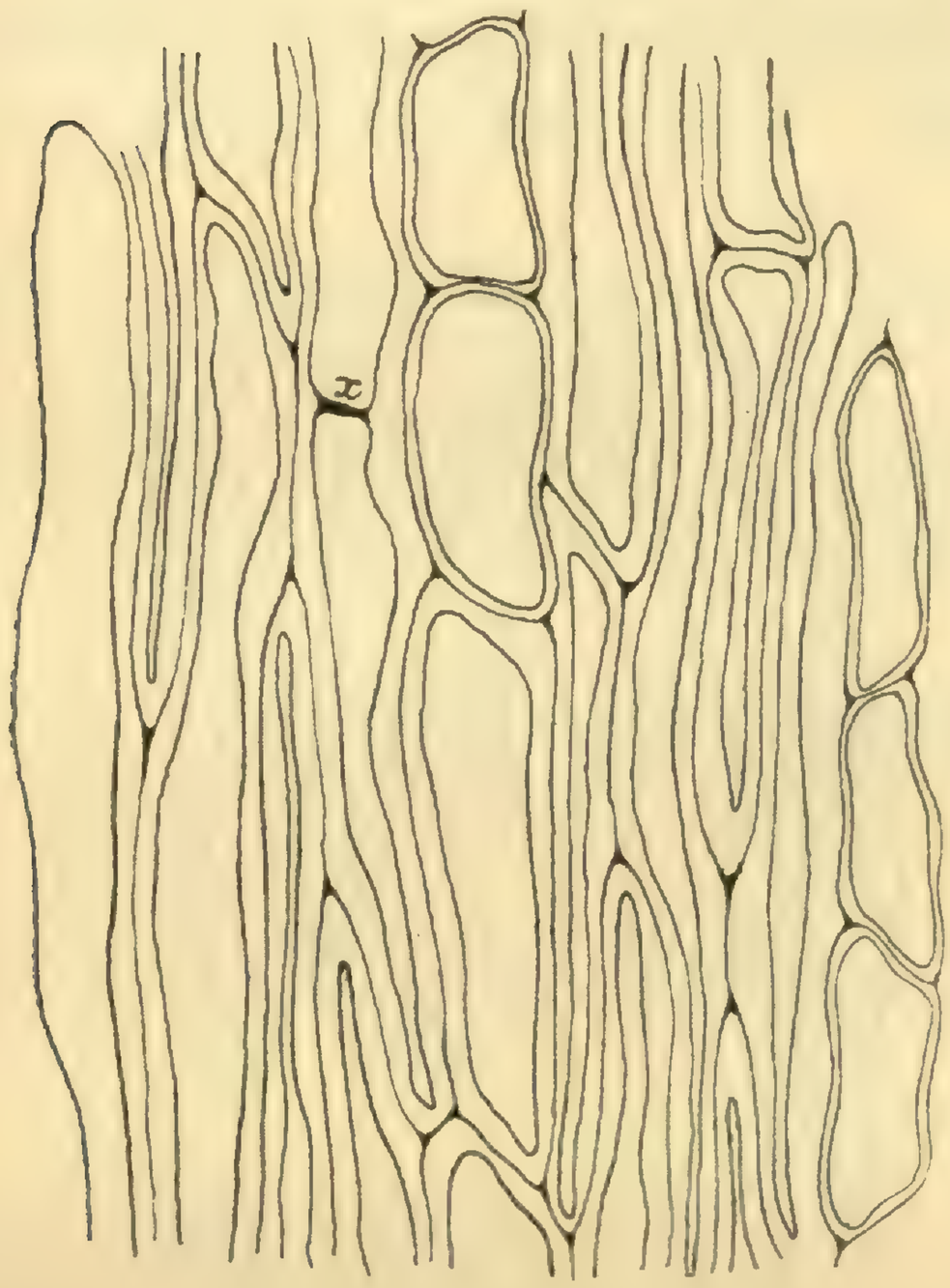
In *C. latifolia*, the elongated thick-walled cells of both upper and lower epidermises are often septate (text-fig. 11); Kraus notes the same fact in *C. Küsteriana*.

C. mexicana shows pitting on the lateral walls of the thickened cells (Pl. 18. figs. 1 & 2). This is more marked on the lower surface than on the upper, especially in the case of the subsidiary cells of the stomatal apertures. In *C. fusco-viridis* also, the lower epidermal cells are much pitted; in *C. latifolia*, however, pitting was not noted, except

* A similar occurrence of crystal-containing cavities is quoted by Nestler in the case of *Encephalartos caffer*. In *D. edule* the cavities are apparently larger than in that species.

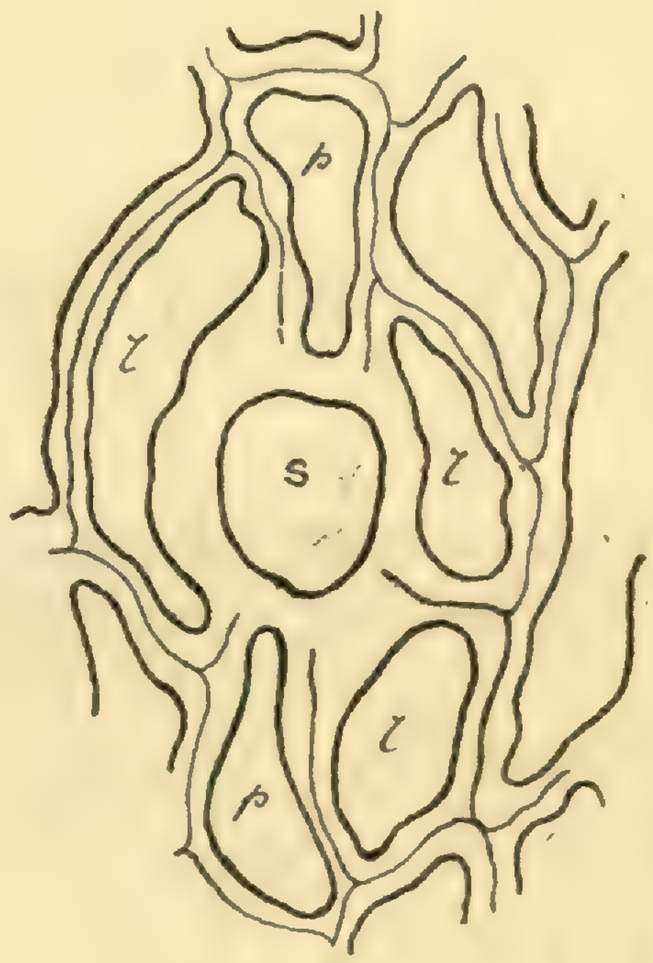
in the cells of the nerve-courses. The cell-walls, particularly in *C. mexicana*, are very strongly layered (Pl. 18. figs. 1–4). *Ceratozamia* has wide stomatal regions and narrow nerve-courses, the demarcation of the areas being most distinct in *C. latifolia*. The stomata lie parallel to the pinna-axis, or somewhat obliquely to it, and are sunk below the level of the epidermis, having one intercalated series of cells (Pl. 18. fig. 4). The air-space is lined with a layer of cutin, extending as is usual to the ventral walls of the guard-cells, and its somewhat oval opening is surrounded by from four to six subsidiary cells; five were observed in *C. latifolia* (text-fig. 12), six in *C. mexicana* (Pl. 18. fig. 2),

Fig. 11.



Ceratozamia latifolia.—Upper cuticle in surface view, showing thin-walled and thick-walled cells. At *x*, an elongated cell is divided by a septum. ×450.

Fig. 12.



C. latifolia.—Lower cuticle (after maceration) in surface view, showing a stoma-opening (*s*) surrounded by five subsidiary cells (*p* and *l*). ×450.

and usually four in *C. fusco-viridis*. Kraus notes four in *C. Küsteriana*. The subsidiary cells do not overarch the air-space to any extent.

The cutin layer is throughout fairly thick, particularly on the upper surface of the leaves (Pl. 18. figs. 3 & 4).

Macrozamia, Miq. Pl. 18. figs. 14 & 15; text-figs. 13–18.

References :—Bornemann (1856), pp. 40, 44; Taf. 11. figs. 16, 17. Schwendener (1881), fig. 13. Nestler (1895), pp. 352, 354; Taf. 12. figs. 10, 11; Taf. 13. fig. 16.

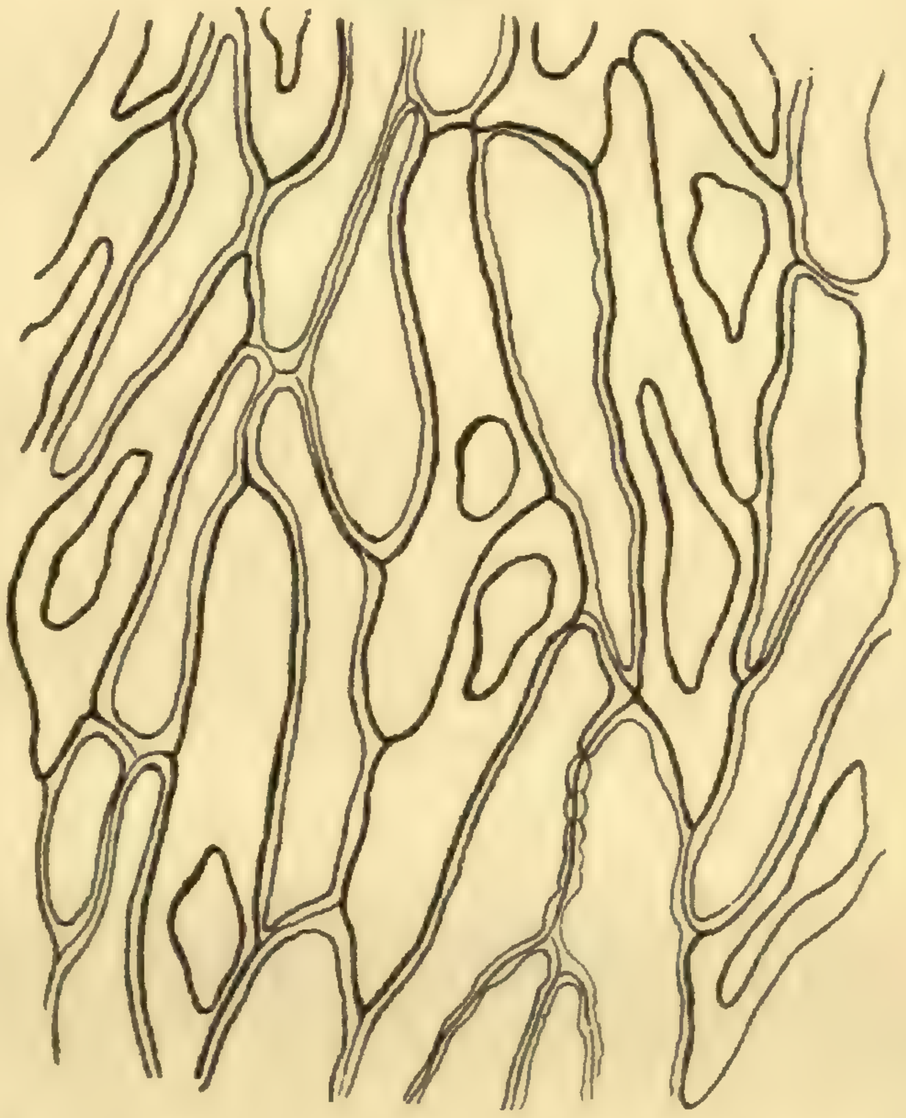
Species examined :—*M. spiralis* (=*Fraseri*, Miq.?); *M. corallipes*, Hook. f.; *M. Denisonii*, F. Muell.: *M. Hopei*, T. Hill; *M. cylindrica*, C. Moore; *M. Macleayi*, Miq. (=*spiralis*, Miq.?).

The six species examined show agreement in the occurrence of thick-walled and thin-walled epidermal cells. They fall into two groups, however, according to the arrangement of the cells. *M. Macleayi* (=*spiralis ?*), *M. Denisonii* (text-fig. 13), and *M. Hopei* (text-fig. 14) differ from the other three species in the irregularly-shaped three- or four-angular cells placed transversely or obliquely to the long axis of the pinna. In this first group, moreover, the thick-walled cells are very marked, their cavities being often almost filled up; there is also a heavy primary wall, particularly in *M. Denisonii* (text-fig. 13). In *M. corallipes*, *M. cylindrica* (Pl. 18. fig. 15), and *M. spiralis* (=*Fraseri ?*) the cells are three- or more often four-angular; they are generally elongated in the direction of the longitudinal axis of the pinna, though the thinner-walled cells are often squarish. In this second group, the walls are often much pitted, particularly in the case of the thin-walled cells (Pl. 18. fig. 15). In the other type pitting is less

Fig. 13.

Macrozamia Denisonii.—Upper cuticle in surface view, showing thin-walled and thick-walled cells, and the heavy primary cell-walls. Note the irregular arrangement of the cells. ×450.

Fig. 14.



M. Hopei.—Upper cuticle in surface view, showing thin-walled and thick-walled cells, and pitting of the thin-walled cells. ×450.

evident. Layering of the cellulose is frequently marked, as in *M. cylindrica* (Pl. 18. fig. 15). The cells of the upper surface and of the nerve-courses of the lower surface are similar in both groups, but the cells between the nerve-courses are usually irregular in shape and size, and are much more uniformly thickened (text-figs. 15 & 16), although occasionally thin-walled cells occur. Sometimes, as in *M. corallipes*, the elongated thickened cells are septate.

Stomata occur only on the lower surface between the nerve-courses; their long axis is parallel with or slightly oblique to the long axis of the pinna. A regular longitudinal arrangement, almost in lines, is seen in *M. spiralis* (=*Fraseri ?*). In all cases the stomata are sunk below the epidermis, an apparently rather irregular system of cells

intervening between the guard-cells and the subsidiary cells. There seem to be typically two series of these intercalated cells (Pl. 18. fig. 14), but the number of series as seen in section through a stoma shows a little variation, apparently owing to irregularity in position of the cells; this is seen in text-fig. 17. In *M. cylindrica* the outer air-space is long, and narrower towards the opening, owing to the slight overarching of the subsidiary cells, which are slightly raised above the level of the epidermis (Pl. 18. fig. 14). The opening as seen in surface view is oval or elliptical in shape. In *M. Denisonii* the outer air-space is shallower and wider (text-fig. 17). In all cases the air-space is fairly heavily lined with cutin. The subsidiary cells vary from five or six to eight in number, but are typically six, as in *M. Denisonii* (text-fig. 15) and *M. Hopei* (text-fig. 16).

Fig. 15.

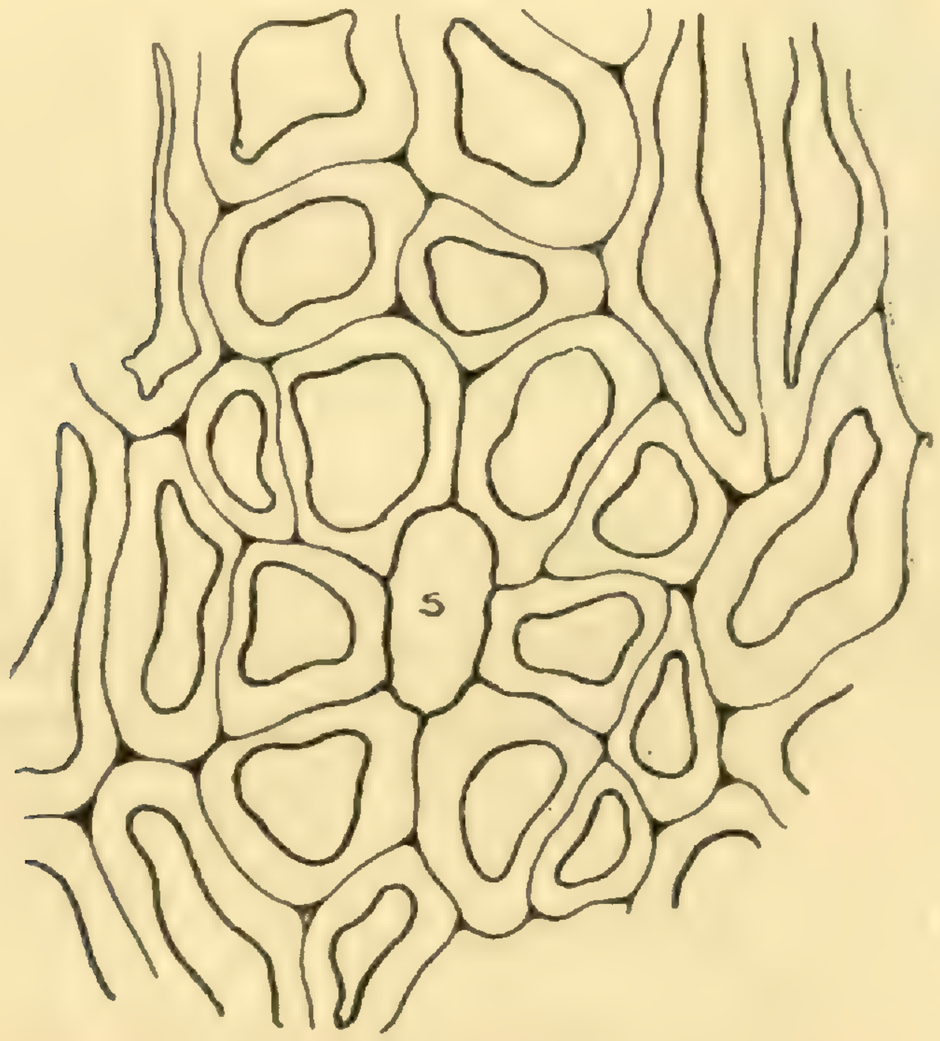


Fig. 16.

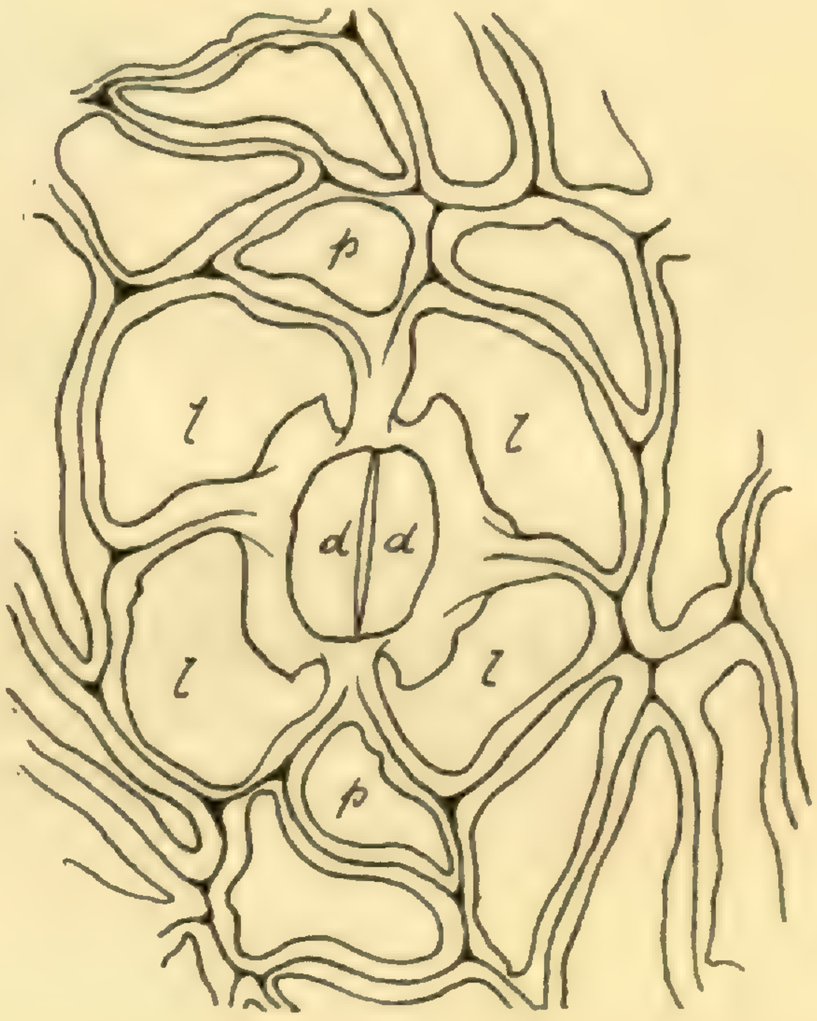
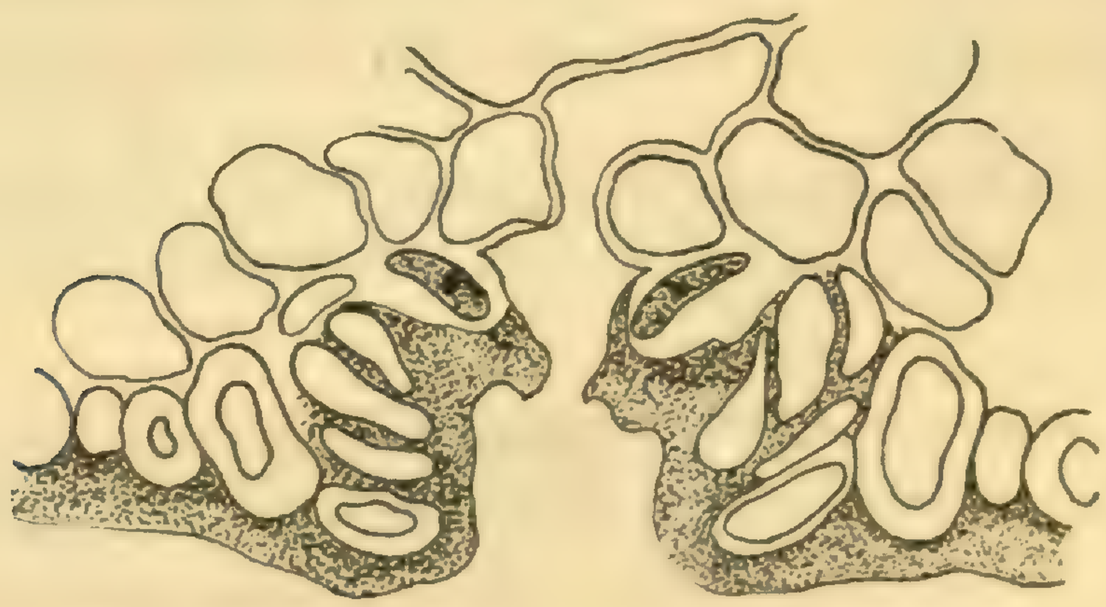


Fig. 17.



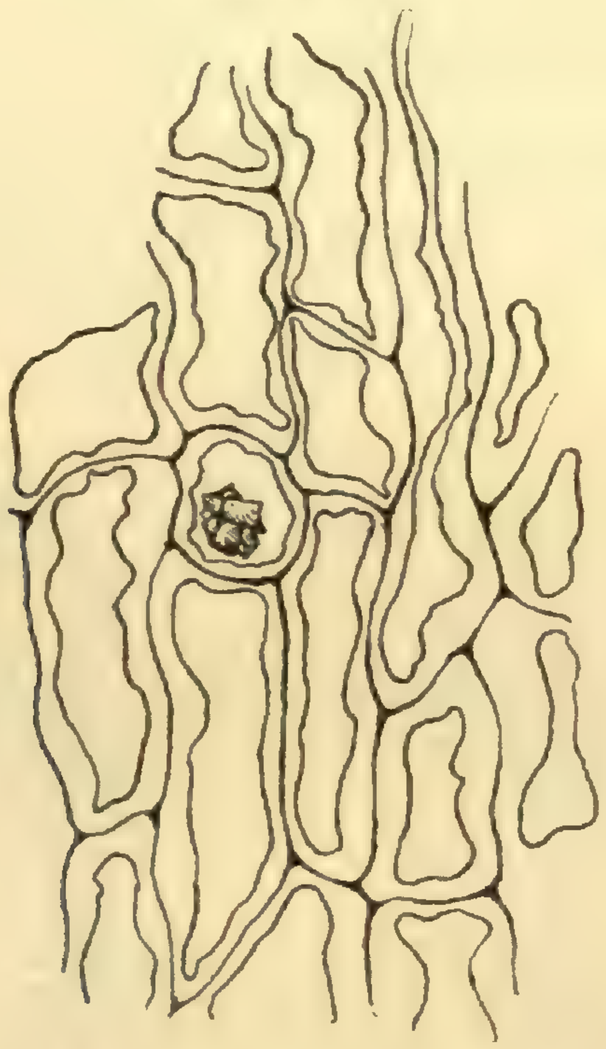
Macrozamia Denisonii.—Lower cuticle in surface view (after maceration), showing stoma-opening surrounded by six subsidiary cells. ×450.

M. Hopei.—Lower cuticle in surface view, showing a stoma-opening with six subsidiary cells (*p* and *l*). The dorsal surfaces of the guard-cells are indicated at *d*. ×450. (This cuticle was not removed by maceration, so that all the thickening of the air-space and guard-cells shows through.)

M. Denisonii.—Lower cuticle, showing a section through a stoma. Note the irregular intercalated cells, between the guard and subsidiary cells. ×450.

In *M. cylindrica*, in the nerve-courses of the lower surface, and also here and there on the upper surface of the pinnæ, occur crystals of calcium oxalate (text-fig. 18); they appear to be contained in small isodiametric cells, and not in cavities, as in *Dioon edule*, and in *M. spiralis* (=*Fraseri?*), where the crystal-containing spaces are very small and not at all frequent.

Fig. 18.



Macrozamia cylindrica.—Lower cuticle (from a nerve-course) in surface view, showing a crystal-containing cell. (*Cf.* the form and arrangement of the cells with those shown in Pl. 18. fig. 15, from the upper epidermis of *M. cylindrica*.) ×450.

The cutin layer is moderately thick (Pl. 18. fig. 14; text-fig. 17), but, as usual, it is thinner on the lower than on the upper surface of the leaves.

Zamia, Linn. Pl. 18. figs. 12 & 13; text-figs. 19–23.

References:—Bornemann (1856), pp. 40, 43, 44; Taf. 11. figs. 7–15. Kraus (1866), pp. 41, 42; Taf. 22. figs. 24–27.

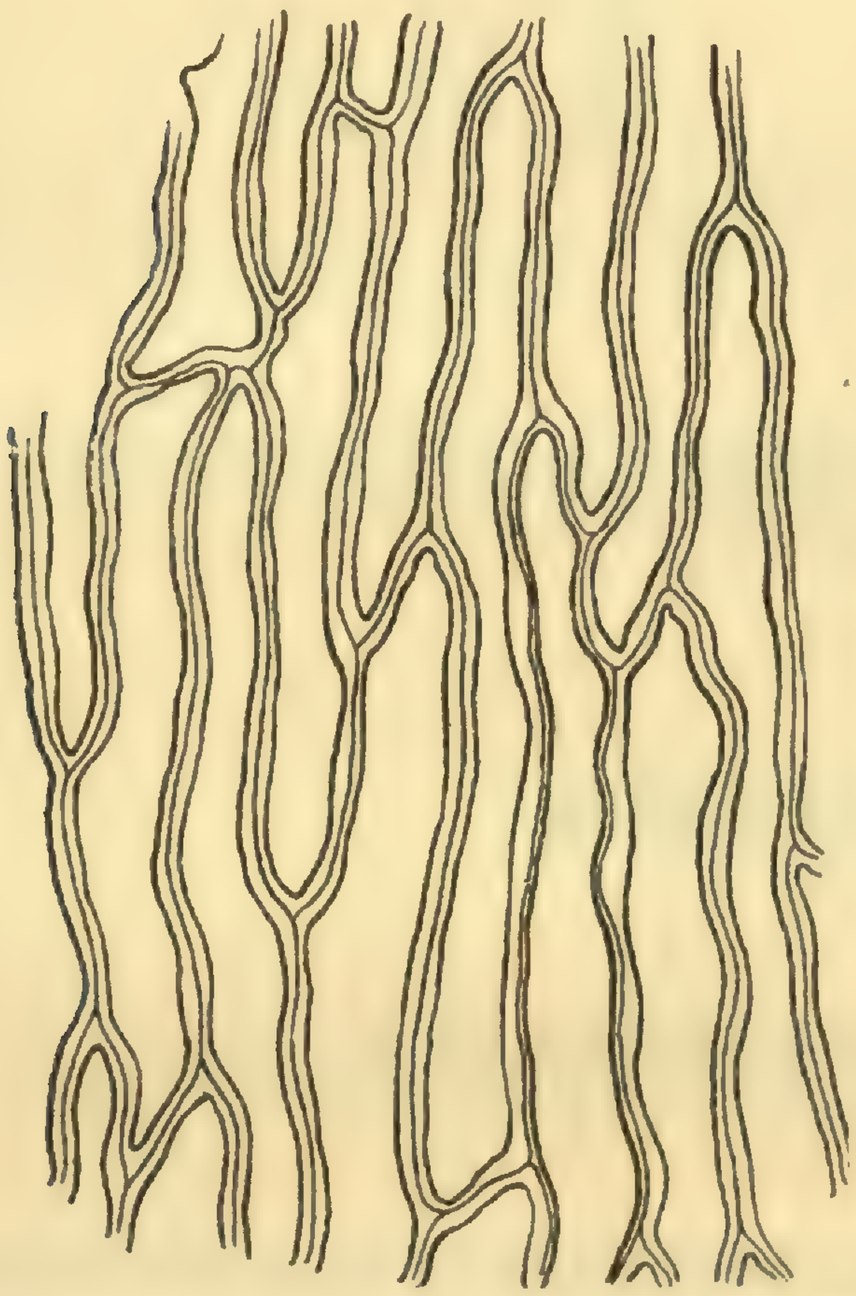
Species examined:—*Z. Skinneri*, Warsz.; *Z. muricata*, Willd.; *Z. Loddigesii*, Miq.; *Z. integrifolia*, Ait.; *Z. Fischeri*, Miq.; *Z. Ottonis*, Miq.; *Z. Lindeni*, Regel,=*Z. cylindrica*, Liebm.(=*Leiboldii*, Miq.?).

These eight species agree in essential characters of the epidermis. The cells in all are elongated in the direction of the longitudinal axis of the pinnæ, and are three- or four-angular in shape. In *Z. Ottonis* the cells are somewhat irregular, with groups of smaller cells here and there. In some species, for example *Z. Skinneri* (text-figs. 20 & 23) and *Z. integrifolia* (Pl. 18. fig. 12), there is a marked distinction into two kinds of cells, thin-walled and thick-walled. In *Z. Skinneri* and *Z. Loddegesii*, the thin-walled cells are only occasional, while the other cells often show a considerable amount of thickening. In *Z. Fischeri* (text-fig. 19) and *Z. Ottonis* the walls throughout are fairly thin. *Z. muricata* has walls of intermediate thickness. The cells of the nerve-courses of the lower epidermis are similar to those of the upper surface. In *Z. cylindrica* and *Z. Lindeni* the cells of the nerve-courses are fairly thick-walled, elongated

and narrow, running quite straightly, and having somewhat pointed ends. The cells between the nerve-courses are shorter and broader and more irregular, but they are still slightly elongated, except in the immediate neighbourhood of the stomata. In the stomatal areas the cell-walls are sometimes thinner than they are on the upper surface; this is best seen in *Z. Skinneri* and *Z. Lindeni*. In *Z. Fischeri* the upper epidermal cells and those of the nerve-courses and stomatal areas are of about the same thickness.

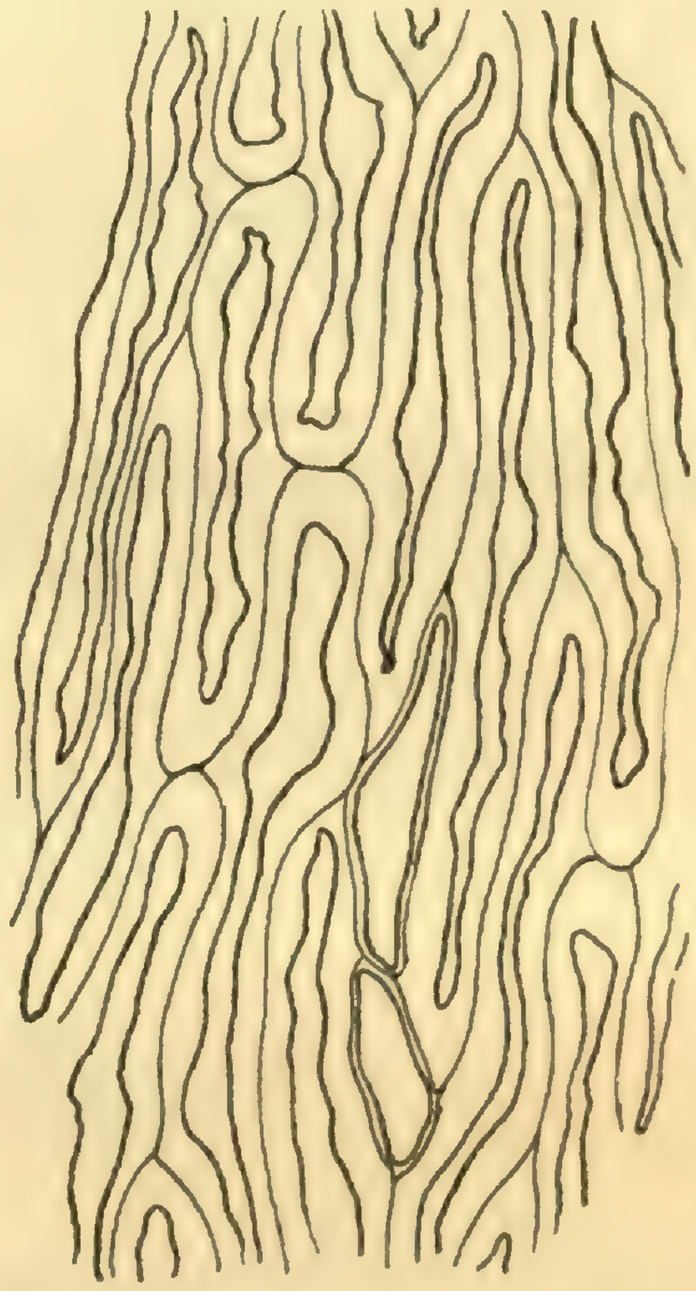
Pittings are sometimes plainly seen (Pl. 18. fig. 12), particularly in the case of the thin-walled cells of nerve-courses. Occasionally the cellulose of the epidermal cells is layered; and in some cases very much elongated cells are septate as in *Z. Ottonis* and *Z. Skinneri*.

Fig. 19.



Zamia Fischeri.—Upper cuticle in surface view. ×450.

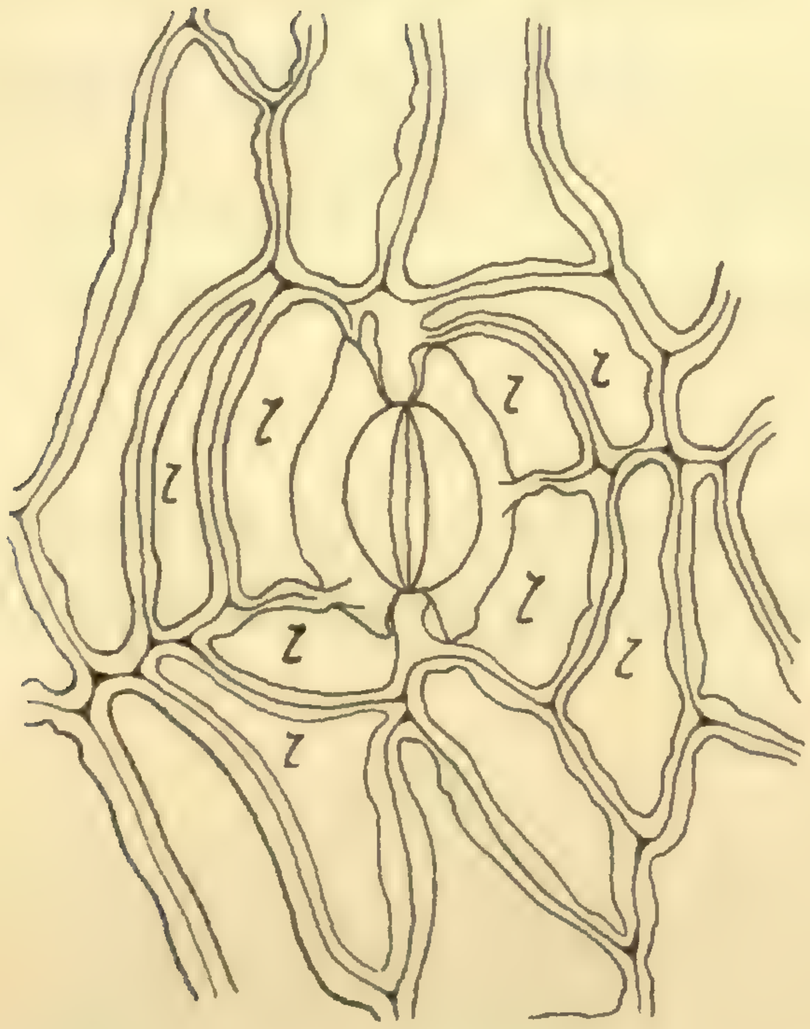
Fig. 20.



Z. Skinneri.—Upper cuticle in surface view. *Cf*. the amount of variation in the thickness of the cell-walls with that shown in text-fig. 19. ×450.

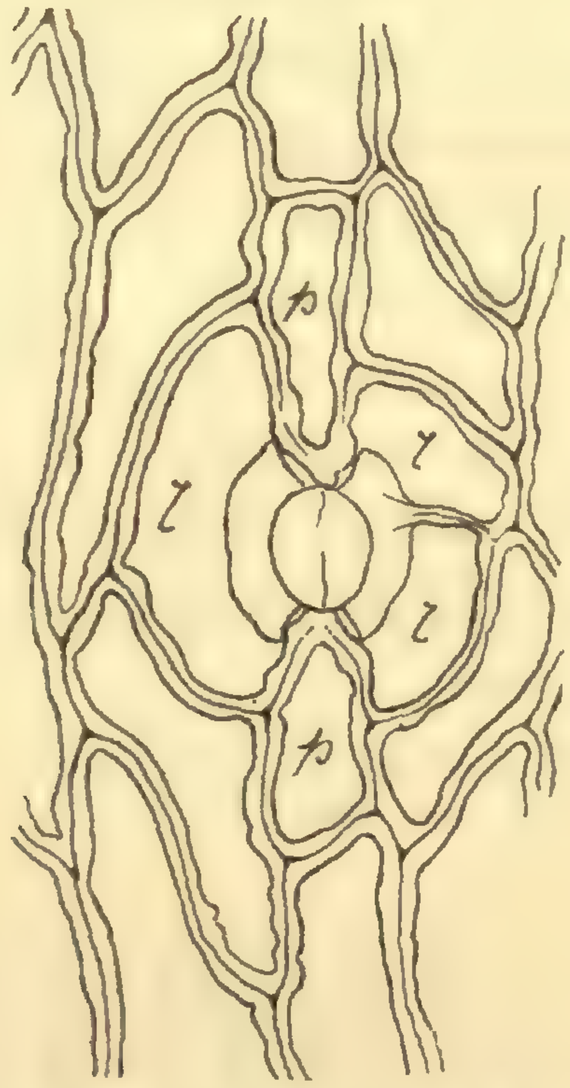
Stomata occur on the lower sides of the leaves in definite areas between the nerve-courses; they are sunk only slightly below the level of the epidermis, there being no intercalated series of cells between the guard-cells and subsidiary cells (Pl. 18. fig. 13). The lignified lamellæ of the guard-cells may be seen, as in *Stangeria* (and *Bowenia*), on focussing slightly below the level of the subsidiary cells. The subsidiary cells are characteristic in number and arrangement; there are from four to six, consisting of an elongated cell at each pole of the stoma, and two (sometimes only one) lateral cells at each side (text-fig. 22). Sometimes a second series of lateral cells is present (text-fig. 21).

Fig. 21.



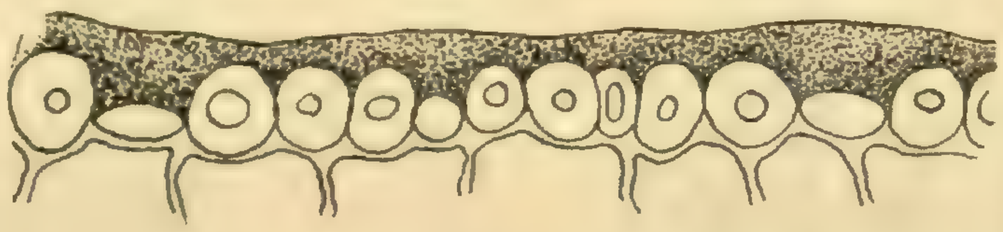
Zamia Lindeni.—Lower cuticle in surface view. The thickened stoma-opening shows a double series of lateral subsidiary cells at each side (*l*, *l*). × 450. (This cuticle was not removed by maceration, and thus shows the thickening substance of the guard-cells and air-space, showing through to the surface.)

Fig. 22.



Z. muricata.—Lower cuticle in surface view. The stoma-opening in this case has five subsidiary cells (*p* and *l*) surrounding it. × 450. (Not macerated; see text-fig. 21.)

Fig. 23.



Z. Skinneri.—Upper cuticle in section, showing the variation in the thickness of the cell-walls. (*Cf.* text-fig. 20.) × 450.

In *Z. integrifolia* hair-scars are occasionally seen, particularly on the under surface in the nerve-courses. The scars seem to occur over a group of the thinner-walled cells. They occur also in *Z Ottonis* and *Z. Skinneri*.

The cutin layer is similar in thickness to that of *Macrozamia* (*cf.* Pl. 18. figs. 13 & 14).

Bowenia, *Hook.* Pl. 17. figs. 7–9; text-figs. 24–26.

References:—Nestler (1895), pp. 356, 357; Taf. 13. figs. 19–21. Porsch (1905), p. 13; Taf. 1. figs. 1–4.

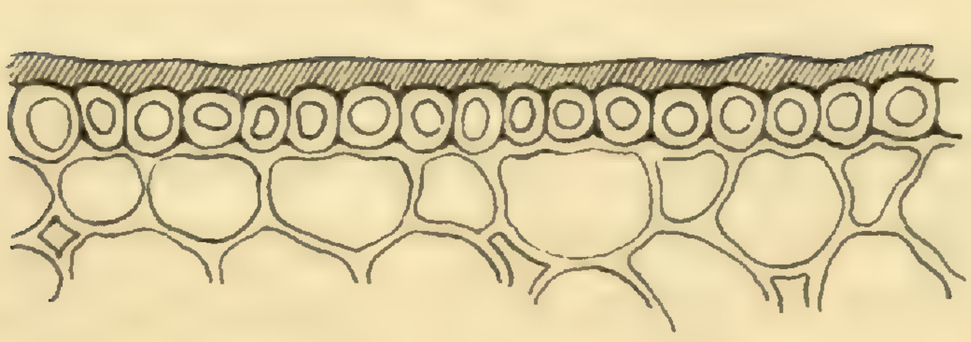
Species examined:—*Bowenia spectabilis*, Hook., var. *serrulata*, André (=*Bowenia serrulata* (André), Chamberlain (1912, p. 419)).

Bowenia serrulata agrees with such Zamias as *Z. Fischeri* in the arrangement of the three- or four-angular epidermal cells and also in the thickness of their walls (*cf.* text-figs. 19 & 25). The cells are elongated, with straight walls, and are slightly narrower

over the nerve-courses, even on the upper surface of the leaf. As is usual, on the lower surface, the cells between the nerve-courses are shorter and broader. No pitting of the walls was observed.

Stomata occur in both the upper and the lower epidermis (Pl. 17. figs. 7 & 8). They are few and scattered on the upper side, occurring principally in the middle of the lower half of the pinnæ, between the veins; they decrease in number towards the upper half and margins. They are fairly abundant on the lower side. In all cases their long axis is approximately parallel with that of the pinnæ. The guard-cells are situated practically at the level of the epidermis (Pl. 17. fig. 9), there being no intercalated series of cells between them [and the subsidiary cells—they are less sunk than those of any other genus except *Stangeria* (*cf.* Pl. 17. fig. 9, *Bowenia*, with fig. 5, *Stangeria*; fig. 14, *Cycas circinalis*; and Pl. 18. fig. 13, *Zamia integrifolia*, for degrees of sinking of guard-cells without an intercalated series of cells). The stomata are surrounded by from four to six subsidiary cells, the walls of which are fairly thin (Pl. 17. figs. 7 & 8), particularly in the case of the stomata of the upper leaf-surface. On account of the position of the guard-cells, *i.e.* almost at the general level of the epidermal cells, the lignified lamellæ of dorsal and ventral walls are plainly seen, giving a characteristic appearance in surface view (Pl. 17. figs. 7 & 8; cf. *Stangeria*, fig. 1). As previously described by Porsch in the case of *B. spectabilis* *, the raising-up of the polar ends of the guard-cells is indicated in surface view by the presence, at each pole of the stoma, of two

Fig. 24.



Bowenia spectabilis var. *serrulata*.—Upper cuticle in section. × 450.

Fig. 25.

B. spectabilis var. *serrulata*.—Upper cuticle in surface view. × 450.

* Porsch (1905), p. 13; Taf. 1. figs. 1 & 3. See also Nestler (1895), Taf. 13. figs. 19 & 20, *b*.

thin pear-shaped areas in the thickened area overlying the guard-cells. The projections of thickening material formed by the extension of the ventral lignified lamellæ are seen at the poles of the stoma (see text-fig. 26, showing the correlation of serial sections through a stoma with the surface view). The cutin layer overlying the lamellæ is faintly striated as in the case of *Stangeria* (Pl. 17. figs. 7 & 8).

Neither hair-scars nor crystal cavities were observed. The cutin layer, compared with that of the other genera, is not very thick (Pl. 17. fig. 9; text-fig. 24).

(iii.) General Summary of the Structure of the Recent Cuticles.

The epidermal cells of Cycad leaves have usually slightly curved or straight walls. *Stangeria* has undulate walls somewhat like those of ferns*. The walls generally attain a considerable thickness, and often show layering as in *Ceratozamia*, *Dioon*, and some Macrozamias. *Bowenia* has comparatively thin walls, while *Ceratozamia* and *Dioon* on the whole have the thickest, though these are characterised by the possession of two kinds of epidermal cells, some elongated and thick-walled, and others shorter and thin-walled. A variation in the thickness of the walls occurs also in *Macrozamia*, some Zamias, and to a certain extent in *Encephalartos*. The epidermal cells are usually elongated, and in *Cycas* and *Stangeria* are alike on both upper and under sides of the leaf. In other types the cells of the under side following the course of the veins are similar, or nearly similar, to those of the upper side, while the general epidermal cells between the "nerve-courses" are more isodiametric. Usually, in the upper epidermis, the nerve-courses are not marked by any difference in the form of the epidermal cells; *Stangeria* shows a slight elongation and narrowing of the cells above the veins.

Stomata occur generally only on the under side of the leaves between the nerve-courses, their long axes coinciding or forming a slight angle with the long axis of the pinnæ. The occurrence of stomata in these definite areas seems to be correlated with the above mentioned difference in the form of the epidermal cells there, as compared with those of the nerve-courses (see *Zamia*, *Macrozamia*, *Ceratozamia*, *Dioon*, and *Encephalartos*). In *Cycas* and *Stangeria* the stomata are scattered and irregularly placed; there are no fixed stomatal areas.

Bornemann (1856, p. 42) has recorded the occasional occurrence of stomata on the upper side of the pinnæ in *Zamia muricata* var. *picta*. Kraus (1866, fig. 15) figures a stoma of the pinna-base in *Encephalartos Altensteinii*; it is apparently from the upper side, though he does not mention the occurrence of stomata other than on the under side of the pinnæ. Nestler (1895, p. 362) was unable to find such stomata in *Encephalartos*; in *Bowenia*, however, he records them from the basal parts of the upper side of the pinnules, gradually decreasing in number and finally disappearing towards the middle. The present investigations have revealed the presence of stomata on the upper side of the pinnæ in *Stangeria*. They are, however, confined to the midrib (text-fig. 1).

* Bornemann (1856), p. 42; Kraus (1866), p. 13.

Nestler (1895, pp. 360, 364) gives a table showing the numbers of stomata per square millimetre in a representative selection of species. The Ceratozamias (with from 24 to 31 per sq. mm.) and the Macrozamias (29 to 31) are seen to have the fewest, and the Dioons (*D. edule*, 81, and *D. angustifolia*, 72) the most numerous stomata. The investigated species of *Cycas* (with from 49 to 56 per sq. mm.), *Encephalartos* (41 to 52), *Stangeria* (54), and *Zamia* (43 to 60) have very similar numerical distribution of stomata, and are intermediate between the Ceratozamias and Macrozamias on the one hand and the Dioons on the other. *Bowenia spectabilis* has 35 stomata per sq. mm. on the under side and 14 on the upper side of the pinnæ.

The stomata of the Cycads as a group are larger than those of any other group of Gymnosperms *. Their size seems to be fairly constant, being about ·075 × ·034 mm., while their structure conforms to a general plan—the "Gymnosperm type" of Porsch. The guard-cells in median and polar section show a constant form and position relative to the general epidermal level.

The ventral and dorsal walls of the guard-cells have in every case lignified lamellæ †, though these are slightly variable in extent and in clearness of definition ‡. They give to those stomata, the guard-cells of which are only slightly sunk, a very characteristic thickened appearance in surface view (Pl. 17. fig. 1, *Stangeria*; figs. 7 & 8, *Bowenia*; text-fig. 26, *Bowenia*). In *Bowenia*, for example, the surface view of a stoma shows the pore bounded on each side by a somewhat crescentic structure formed by the lignified lamellæ on the upper or dorsal surface of the guard-cell. This is covered by a layer of cutin. The lamellæ on the lower or ventral surface of the guard-cells are only seen at the poles of the stoma, where the guard-cells are raised and the lamellæ are extended, appearing as thickened projections. Text-fig. 26 shows the correlation of serial sections through a stoma with the surface view. The gradual raising of the guard-cells towards the poles and extension of the ventral lamellæ with accompanying diminution of the dorsal lamellæ are plainly seen. In the case of guard-cells which are much sunk, the surrounding, and usually overarching, epidermal cells obscure the characteristic appearance caused by the lignified lamellæ. In intermediate conditions such as exhibited by *Zamia* (Pl. 18. fig. 13), the lamellæ of the guard-cells may be seen on focussing slightly below the epidermal cells. They are quite comparable with those of *Bowenia* and *Stangeria*.

The epidermal cells surrounding the guard-cells and stoma-opening—"subsidiary cells"—are usually fairly constant in number and arrangement in a genus. In no case was material available young enough to trace the entire development of the guard-cells and subsidiary cells from an epidermal mother-cell. Four seems to be the original number of subsidiary cells, the typical arrangement of these being one at each pole of the stoma and one at each side. It seems possible from a comparison with *Gnetum* and *Welwitschia* §, together with a consideration of fairly young examples in *Cycas revoluta*

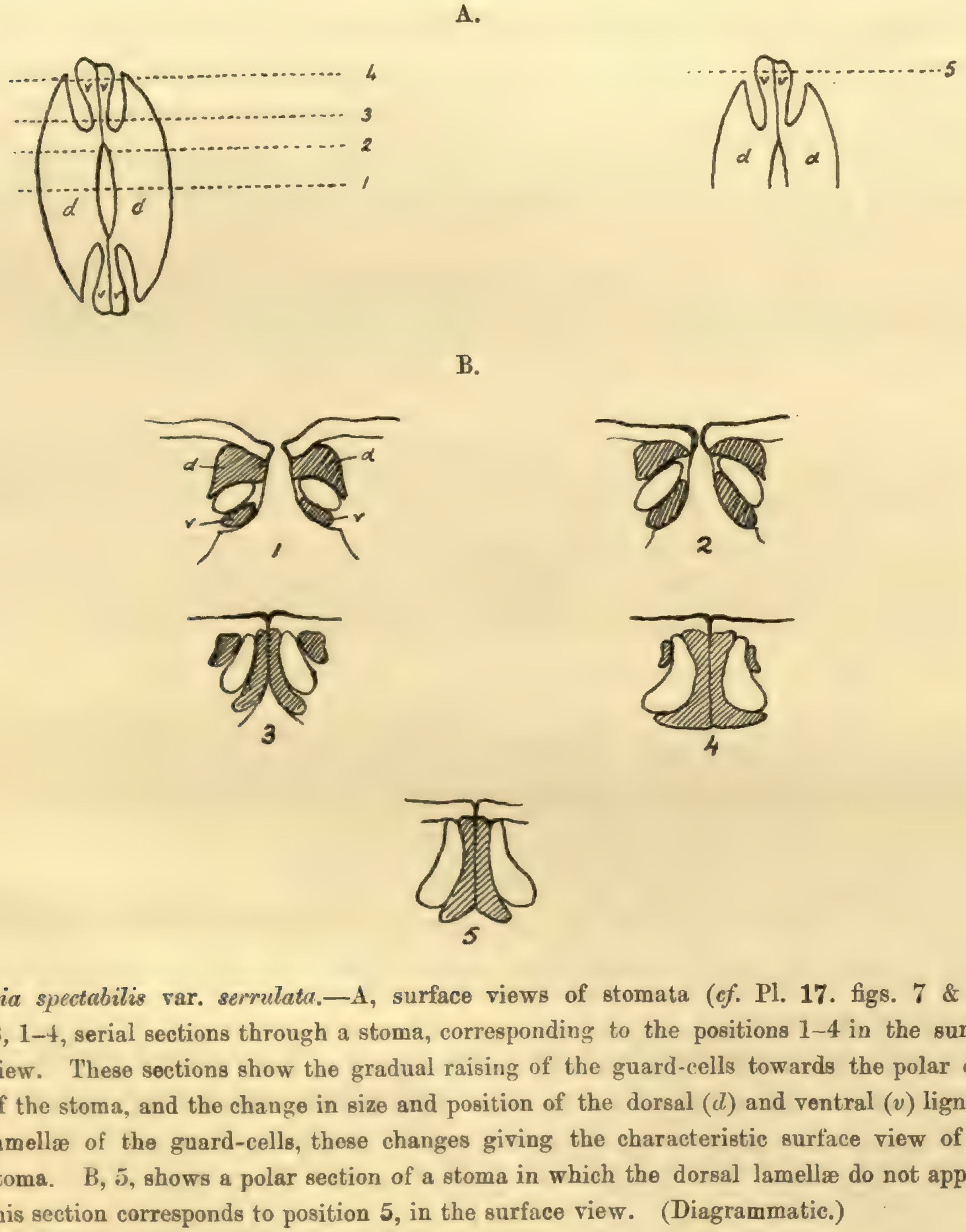
* Malhert (1885), p. 57.

† These are not figured in every case; they are shown in text-figs. 10 & 26 and in Pl. 18. figs. 4 & 6.

‡ Karzel (1908). § Takeda (1913[1]), p. 351; & (1913[2]), pp. 365, 366, text-fig. 8.

and *Ceratozamia mexicana*, that the polar subsidiary cells represent ordinary epidermal cells, while the lateral ones are the product of division of the epidermal mother-cell giving rise to the guard-cells also. Frequently the lateral cells are transversely divided into two, so that six subsidiary cells — two polars and four laterals — are seen. Occasionally only one of the lateral cells is divided; division of the polar

Fig. 26.



Bowenia spectabilis var. *serrulata*.—A, surface views of stomata (*cf.* Pl. **17**. figs. 7 & 8); B, 1–4, serial sections through a stoma, corresponding to the positions 1–4 in the surface view. These sections show the gradual raising of the guard-cells towards the polar ends of the stoma, and the change in size and position of the dorsal (*d*) and ventral (*v*) lignified lamellæ of the guard-cells, these changes giving the characteristic surface view of the stoma. B, 5, shows a polar section of a stoma in which the dorsal lamellæ do not appear; this section corresponds to position 5, in the surface view. (Diagrammatic.)

cells is comparatively infrequent. An increase in the number of subsidiary cells is often seen where guard-cells are much depressed below the general level of the epidermis, there being a mechanical necessity for this increase—the deeper the outer air-space, the greater the number of cells required to ensure its rigidity, by means of their lateral walls.

In *Bowenia* and *Stangeria*, where the guard-cells are not sunk, there are from four to six subsidiary cells, differentiated into polar and lateral (text-fig. 1; Pl. 17. figs. 1, 7, & 8). Occasionally there is some displacement of the cells, so that the differentiation is not always quite definite (text-fig. 1; Pl. 17. fig. 8). *Encephalartos* (text-figs. 7 & 8), *Ceratozamia* (text-fig. 12; Pl. 18. fig. 2), *Macrozamia* (text-figs. 15 & 16), and *Zamia* (text-figs. 21 & 22) typically show from four to six subsidiary cells, differentiated into polars and laterals. An interesting distinction in *Zamia* is the frequent presence of a second series of lateral subsidiary cells, parallel with the first, due perhaps to the longitudinal division of the original lateral cells * ; this is well seen in *Zamia Lindeni* (text-fig. 21). The subsidiary cells in these four genera are at a different level from that of the guard-cells, the latter being sunk to a greater or less degree, forming an outer air-space. The opening of the air-space at the surface of the leaf is elliptical to quadrangular in shape. In some cases, particularly in some Macrozamias and some species of *Encephalartos*, there is a certain amount of overarching of the subsidiary cells. In cases where the guard-cells are much sunk, the opening of the air-space on the leaf-surface is more rounded in shape, and the subsidiary cells, which tend to increase in number for the better strengthening of the large air-space, are not distinguished into polars and laterals. This is seen in *Dioon* and *Cycas revoluta*, where all the cells are of the same shape. Occasionally also the subsidiary cells are raised beyond the general level of the epidermis, forming small elevations perforated by the stoma-openings (Pl. 17. figs. 12 & 13, *Cycas revoluta*).

In some cases crystals of calcium oxalate occur in the epidermal layers; in *Stangeria* they are to be found in the cells round the stomata; in *Macrozamia cylindrica* crystals occur on the upper leaf-surface and on the lower surface in the cells of the nerve-courses. In other cases, e. g. *Dioon edule* and *Macrozamia spiralis* (=*Fraseri ?*), they occur in spaces between the epidermal cells.

Hair-scars occur in several cases, such as *Encephalartos Ghellinckii*, *Cycas circinalis* and *C. revoluta*, *Zamia integrifolia* and *Stangeria*.

The cutin layer overlying the epidermal cells is fairly thick—usually thicker on the upper than on the under side of the leaf. *Dioon*, *Ceratozamia*, and some species of *Encephalartos* show the heaviest cutin layer, while that of *Bowenia* is comparatively thin. The cutin of *Stangeria* has very characteristic folds.

III. CUTICLES OF FOSSIL CYCADEAN FRONDS.

(*a*) Previous Observations on the Cuticular Structure of Fossil Cycadean Fronds.

Bornemann, whose work has been mentioned above, was the first to make observations upon the structure of the cuticles of fossil fronds, and, in fact, made a comparative study, based on the recent forms, of a type which has never since been attempted (1856). The

* *Cf.* Takeda (1913 [1]), p. 351; (1913 [2]), pp. 365, 366; text-fig. 8.

fossil remains with which he had to deal were, however, very fragmentary; little or nothing could be made out as to the macroscopic characters of the fronds whose cuticular structure is figured, and from his figures one is led to suppose that the preservation of the fragments or the methods of treatment were not of the best. In the cases figured the walls of the epidermal cells are all represented as straight, and the stomata figured do not allow any close comparison with the examples now before us. It would appear that the forms figured on his Taf. 7. figs. 1–6 are allied to *Thinnfeldia*, but in no other cases are the stomata sufficiently well represented.

Schenk, in his Fossil Flora of Frankonia (1867), made a great advance in the study of cuticles; he described and gave accurate figures of the cuticles of a number of forms, including *Tæniopteris stenoneura*, *Thinnfeldia* spp., *Nilssonia polymorpha*, *Otozamites* (*Otopteris*) *Bucklandi*, *Pterophyllum* spp., several conifers and ferns. He does not give many good figures of preparations showing stomatal structure, but he was the first to observe the sinuous walls of the cells in various species of *Pterophyllum* and in *Otozamites*. He mentions that he has made preparations from the English species *O. acuminatus*, *O. Beani*, and *O. graphicus*, also of the English species of *Tæniopteris*, which was found to be comparable with the Otozamitean structures *. He gave some short descriptions of stomata, noticing that they occur usually on one side of the lamina only; but there are many points of importance on which we can obtain no information from his work. The same author subsequently figured the cuticles of *Dioonites Dunkerianus* (Goep.) †.

Zeiller (1882) described and figured the epidermal structure of a *Thinnfeldia* (*Cycadopteris Brauniana*) and *Frenelopsis Hoheneggeri*; he has also figured a small piece of a cuticle of a Palæozoic *Pterophyllum* (Zeiller, 1906).

In his 'Jurassic Flora of the Yorkshire Coast' Prof. Seward (1900, p. 234, fig. 43) has given a good figure of part of a lower cuticle of *Ctenis* sp. The form of the epidermal cells, often bearing papillæ, was well shown; the stomata were not clearly seen, but there were depressions representing the cavities in which the stomata were sunken.

Most of the recent observations on the epidermal structures of Mesozoic Cycadean fronds have been made by Prof. Nathorst. He has described and figured the cuticles of species of the following genera:—*Dictyozamites*, *Pseudocycas*, *Ptilozamites* (*Ctenozamites*), and *Nilssonia* ‡. He has given many excellent photographs of these, but has not yet paid special attention to the structure of the stomata, which is one of the most important features from the point of view of the present inquiry. As will be seen later, many of the cuticles now described and figured can be very closely compared with the specimens from the Scandinavian plant-beds. This is especially the case in the instance of *Dictyozamites Johnstrupi* from Bornholm and *Dictyozamites Hawelli* from Marske. The close similarity between these forms, and also the similarity between specimens of other types occurring in both the Lower and Middle Estuarine beds of different parts of North

* Schenk (1867), p. 165.

† Schenk (1871), pl. xv. figs. 2–4.

‡ Nathorst, Paläobotanische Mitteilungen i.–iv., 1907–8; and 'Ueber die Gattung *Nilssonia*,' 1909.

Yorkshire, indicate that the cuticular structures are not essentially affected by purely local conditions, but show characters which are related to the more general conditions and also to questions of phylogeny.

More recently Prof. Nathorst (1912, p. 36) has given a short summary of the results of his cuticular work, and has arranged the genera which have been studied in five groups or orders characterised by the following forms:—(a) *Pterophyllum*, (b) *Otozamites*, (c) *Pseudocycas*, (d) *Nilssonia*, (e) *Ptilozamites*. He does not give a detailed description of the characters of the cuticles of these orders, and they appear to be somewhat unequal in value. He thinks that classes (a), (b), and possibly (c), belong to the Bennettitales, while (d) and (e) are more related to the modern Gymnosperms.

For the purposes of comparison with another group of Jurassic Gymnospermous plants, the excellent figures of stomata of some genera of Ginkgoales given by Prof. Seward * are very useful. The Ginkgoales possess a very definite and constant type of stomatal structure which is somewhat similar to that found in some Nilssonias.

(*b*) Detailed Descriptions of the Cuticular Structure of some Fossil Cycadean Fronds.

I. Bennettitales.

Ptilophyllum (Williamsonia) pecten (Phill.), n. comb.

The large and somewhat variable group of fronds usually placed in the aggregate species *Williamsonia pecten*, can now be divided into several sections according to the structure of their epidermal cells. The smaller type of frond with regular straight linear or linear-lanceolate pinnæ, closely approximated and attached by almost the whole length of their bases, can be distinguished from the larger type with broader pinnæ, which are slightly falcate, more truncated at the apex and contracted at the base, and with a somewhat more spreading venation. So far as can be seen from external appearance, these two types seem to be connected by a series of gradations, as may be noticed in the figures given in Prof. Seward's 'Fossil Flora of the Yorkshire Coast,' where pl. 3. fig. 1 resembles the small type, and pl. 3. fig. 6 probably represents a frond of the larger type (the differences mentioned above are, however, much more noticeable in other examples from Marske and Whitby collected by one of us). When cuticular preparations are made, the two types of frond can be readily distinguished by the presence or absence of large numbers of thickened circular markings arranged in rows on the cuticles of the second form. These, as mentioned later, were probably of the nature of the thickened bases or scars of hairs of which no trace is seen externally without considerable magnification. The fronds possessing these curious markings, as well as other slight differences, must probably be placed in a new species. The separation of these two types probably involves the distinction of a third and larger type of frond, and the recognition that the three forms from Marske, figured recently by one of us (Thomas, 1913), are probably three

* Seward (1911[1]), pl. 4. figs. 56, 57 ; pl. 5. figs. 58–62 & 64.

distinct species. We cannot here enter into this question in detail, but it may be remarked that the existence of several species of fronds is rendered probable by the discovery of a number of different species of male and female flowers which probably belonged to some of the plants bearing these *Ptilophyllum* fronds. Three or four forms of male flowers and five or six species of female flowers of the *Williamsonia* type are now known. Besides these we know of two or three other types of flower which probably belonged to plants bearing fronds of some of the other forms placed in the Bennettitalean group in the present paper. In view of the uncertainty of connecting "flowers" with fronds, it appears to be better, at present, to use the generic term *Williamsonia* to apply only to reproductive structures, while referring to the fronds under the names of their form genera. Thus we shall refer to *Williamsonia pecten* (Phill.) fronds as *Ptilophyllum pecten* and to *Williamsonia gigas* fronds as *Zamia gigas*, Lindl. & Hutt.

We may now proceed to the description of the cuticles of fronds of *Ptilophyllum pecten* (Phill.) *. The cuticles of the upper and lower epidermis are very distinct (see Pl. **20.** fig. 1). The upper epidermis is composed of uniform cells showing no traces of veins and having no stomata. The walls of the cells show an extremely sinuous outline, a characteristic in the Bennettitalean group; each wall is bent into a regular series of folds which sometimes almost touch each other. The appearance of this cuticle is seen in the photograph reproduced on Pl. **20.** fig. 2.

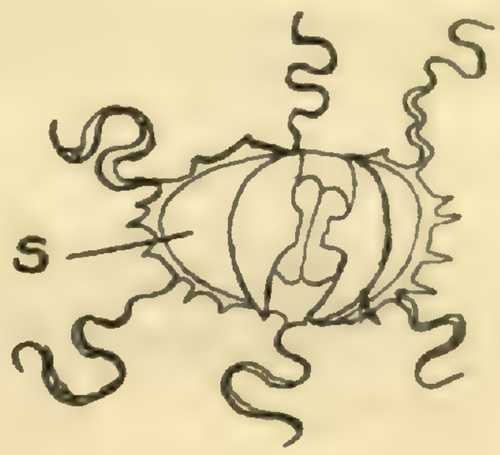
The lower epidermis is composed of cells with a somewhat similar outline, usually rather thinner than those of the upper epidermis and with larger lumina. There is a marked differentiation between the areas above the veins which possess no stomata and the intermediate portions where the stomata occur in two or three rows (Pl. **20.** fig. 1). The cells above the veins exhibit a somewhat more elongated form than the rest. A few circular hair-scars are sometimes seen. Near the margin of the leaf the cells become more elongated and their walls thicker.

The Stomata.—In each square millimetre of the lower surface between 50 and 60 stomata occur; this number seems fairly constant in the specimens examined. The individual stomata are roughly circular, with a diameter of about ·039 mm. The guard-cells are very regularly orientated, so that the slit lies transversely, at right angles to the veins of the pinna. The regular arrangement of the stomata is a characteristic feature of the *Ptilophyllum-Otozamites* group of fronds; in other genera they are irregularly scattered. The guard-cells do not seem to be appreciably sunk. On either side they have a small subsidiary cell (*s*, text-fig. 27), on to which the sinuous walls of the epidermal cells abut. The actual structure of the guard-cells is somewhat difficult to make out from the surface view of the remains of their cuticularised portions (Pl. **20.** fig. 3). From the analogy of the modern stomata (*cf.* text-fig. 26) it seems probable that the structures seen in our preparations do not represent the outlines of the cells round the stomatal pore but only parts of their walls which were differently thickened at

* For methods of obtaining cuticular preparations see Thomas (1912), also Nathorst (1912) and Bather (1908). In this section the term cell-wall is used for the ridges on the cuticular film which now represent the walls of the original cells.

two levels. The appearance observed when preparations of stomata are seen in surface view (text-fig. 27; Pl. 19. fig. 1) is as follows:—On either side of the central slit-like pore are two elliptical or hemispherical structures; they are somewhat flattened where they abut the pore, and have rounded ends, appearing, in fact, rather like an ordinary guard-cell appears in surface view. Between these and the subsidiary cells lie two other thickened patches, more or less hemispherical in shape, and apparently somewhat overlying the central structures. They possess a very characteristic outline, and have, like the central ones, a deep brown colour; they often show peg-like extensions towards the centre (see text-fig. 27). Very similar patches are seen in almost all the stomata of this group. They often have a slightly shorter diameter (measured in the polar plane) than the subsidiary cells, but are longer than the central structures; in some cases they appear to be attached to the latter, but in other preparations appear to be free from them at the ends, only lying over them in the centre (*cf.* Pl. 19. fig. 1).

Fig. 27.

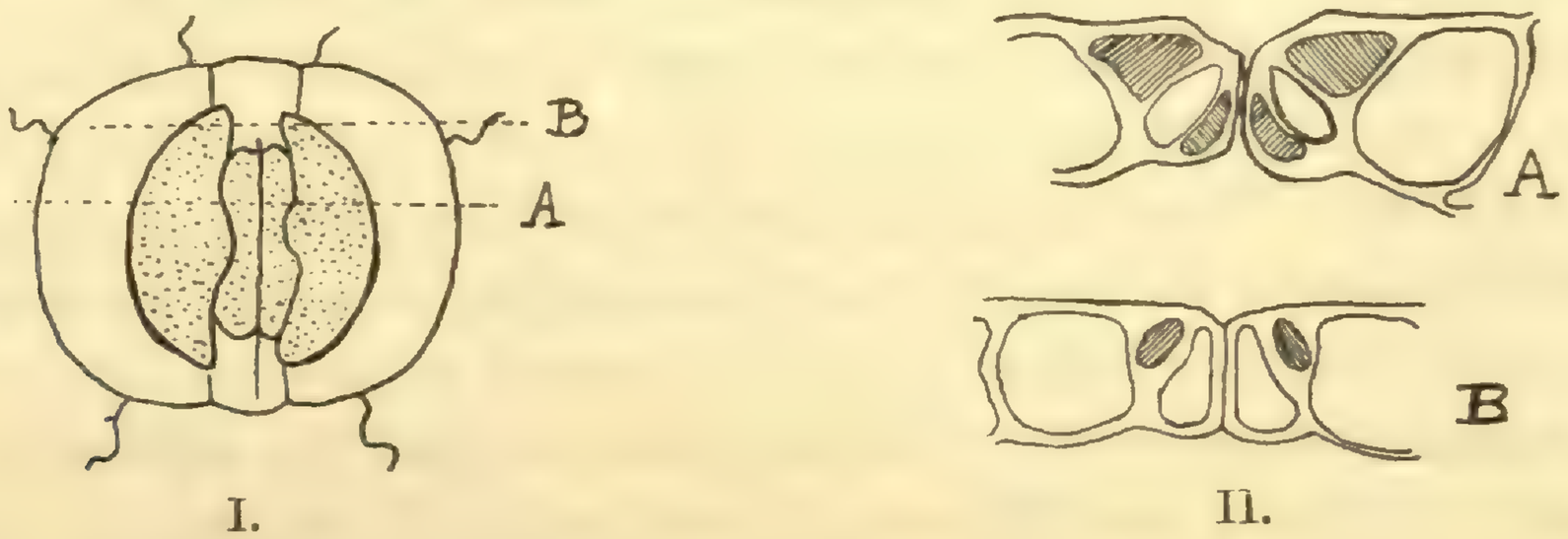


Stoma of *Ptilophyllum pecten*, showing subsidiary cells (*s*) and thickenings of guard-cells.

The interpretation of these structures would be somewhat difficult but for our knowledge of the thickenings possessed by the guard-cells of modern forms. In the surface view of these we never see the outlines of the guard-cells, but only the form of their thickenings or woody lamellæ. In *Bowenia* the thickening on the upper face of each guard-cell forms a hemispherical structure at each side of the pore, while the lamellæ on the lower faces contribute the projecting pieces seen at the poles (*cf.* text-fig. 26). In the present case we seem to be dealing with a very similar structure. It is clear that the central patches bordering on the slit do not represent the actual guard-cells. They are often extended into sharp points at the poles, are much smaller than the subsidiary cells, and do not abut directly on to them; moreover, on this view the presence of the intermediate patches cannot be easily explained. It seems likely that we see in the fossil fronds two pairs of thickening patches or lamellæ belonging to the upper and lower sides of the original highly inclined guard-cells. These lamellæ were somewhat similar to the woody lamellæ of the modern forms, but were more strongly cutinised. The central lamellæ would be originally on the lower side of the cells and would be much shorter than in the modern structures. The outer and more thickened patches would represent the upper lamellæ of the guard-cells, which, however, overlapped the lower lamellæ to a much smaller extent than in *Stangeria* and *Bowenia*, but are almost identical in shape

and in their relations to the subsidiary cells, with the thickenings of *Stangeria* seen after maceration (see text-fig. 32). The figures below (text-fig. 28) show an attempt to reconstruct the sectional views of the stomata at various points in accordance with the explanation given above.

Fig. 28.

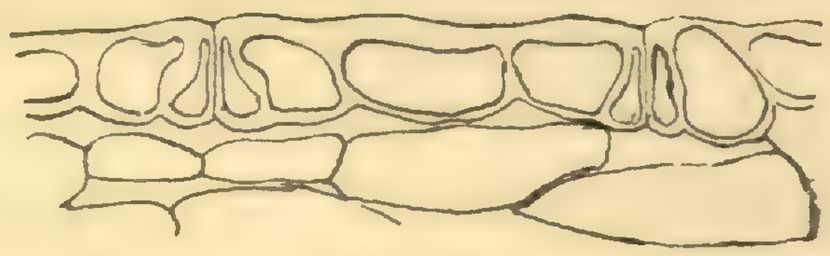


Diagrams representing surface view of stoma of *Stangeria* (I.), with hypothetical sections (II.) at the different points indicated in I. The shaded and dotted portions represent the probable positions of the thickened portions.

In some modern stomata we find that the upper lamellæ do not extend unchanged to the pore, but the latter is surrounded by a thinner oval area. A precisely similar arrangement is seen in some of the *Ptilophyllum* and *Zamia* cuticles (see Pl. 19. fig. 2).

Unfortunately, it has proved impossible to obtain sections through the cuticles showing the structure of these stomatal remains, but a comparison of the material before us with the stomata figured by Lignier provides some interesting features and gives considerable support to the interpretation just advanced. In his paper on *Bennettites Morierei*, Lignier * observed that in some sections through the involucral bracts, the stomatal guard-cells, cut through transversely, were seen. In one of his figures, Pl. 1. fig. 9, which is reproduced below (text-fig. 29), two stomata are seen in

Fig. 29.



Section through the epidermis of a bract of *Bennettites Morierei* showing two stomata cut through. The characteristic form of the guard-cells and subsidiary cells is well shown. (After Lignier.)

section cut through transversely somewhat near their poles. The guard-cells are seen to have the pear-shaped outline, so characteristic of the modern forms (*cf.* text-figs. 26, etc.), with a marked upward extension. The upper walls of the guard-cells are drawn as being somewhat thickened, the wall abutting on the slit being thin;

* Lignier (1894), p. 18, pl. 1. figs. 8, 9.

on either side of the guard-cells are two well-marked subsidiary cells. The figure further shows that the guard-cells of adjacent stomata were approximately parallel to each other, and that the inclined guard-cells became more vertical at the poles and their upper or outer thickening became less. In figure 8 of the same plate another stoma is shown cut through more or less longitudinally, but the section has not here passed through the centre. No stomata were seen in surface view, but in a later paper * surface views are given of stomata from the interseminal scales of the same specimen, which had been obtained by collodion casts. Though the details are not very clearly shown, it is evident that these stomata were of the same type as those which are described here, the guard-cells and subsidiary cells of some of them being quite characteristic. The structure of these stomata in Lignier's species of *Bennettites*, a genus closely allied to our Yorkshire *Williamsonia*, not only provides an interesting and very close comparison with the modern *Bowenia* type, but also goes some way towards demonstrating that the interpretation which we have given above, of the meaning of the surface views of stomata in this group, is correct.

We have dealt at some length with the structure of these *Ptilophyllum* stomata because the form of these organs is remarkably constant throughout the group of fronds which we have assigned to the Bennettitales. Moreover, their appearance is so complex that at first sight it is very difficult to understand them; no previous observers seem to have made any attempt to grapple with the problem, but have merely spoken of the thickening patches as the guard-cells.

Ptilophyllum sp.†

Typical examples of *Ptilophyllum pecten*, from the Lower Estuarine beds of Whitby and Marske, show perfectly smooth cuticles with very few hair-scars. In the larger fronds, however, from the same beds, a large number of very characteristic structures are seen, which are also present on the fronds of the small *pecten*-form which occur plentifully in the Cloughton Wyke beds of Middle Estuarine age.

These structures are shown in Pl. 20. fig. 4. They may be described as small annulate projections from the surface of the cuticle ·03 to ·04 mm. in diameter, occurring in numerous regular rows running parallel to the length of the pinna. The rows are very close together, being often separated by a space less than their individual width. The annulate structures of the same row are frequently contiguous and are sometimes unevenly thickened, being broader and darker laterally and thinner at the points next to the adjacent rings, so that an appearance is produced of pairs of crescentic patches. They are so numerous as to obscure entirely the outlines of the epidermal cells and make the stomata very indistinct.

We may regard these structures as the bases of hairs, with which the lower surface of the frond was covered. Scattered hair-scars occur on the ordinary types of frond, which

* Lignier (1912), p. 426, fig. 1.

† This species will later be described as *Ptilophyllum hirsutum*; a figure of typical outline of a frond is given in the 'Fossil Flora of the Marske Quarry,' text-fig. 3 B. Thomas (1913).

do not differ markedly from those on some modern Cycad fronds, but they are not so massive as in the present example, nor are they arranged in such a regular sequence. When, however, the epidermal cells are arranged in regular rows, the outgrowths from them may be expected to possess the regular arrangement which we see here. The fronds just mentioned appear to possess stomata which are somewhat similar to those above described (see text-fig. 30).

An interesting comparison can be drawn between the hair-scars seen so abundantly on these fronds, and the hairs on the bracts and lower part of the strobilar-axis in the flower of *Williamsonia scotica*, recently described from the Kimmeridge of Sutherland by Prof. Seward *. The hairs in the latter formed a very striking feature; they were very numerous, and arose from the thickly cuticularised outer wall of an epidermal cell which formed a dark ring round the lower end of the hair. Higher up the walls of the hair were much thinner. If leaves bearing hairs of this type had been preserved as impressions in the same way as the material now before us, we could scarcely expect the substance of the hair to be preserved, though the cuticularised base would remain as

Fig. 30.

Stomata of *Ptilophyllum* sp., showing form of the guard-cell thickenings.

a clearly visible ring on the outside of the epidermis. It is possible, too, that hairs of this type might have been deciduous. The occurrence of these characteristic hair-scars forms another link connecting the *Ptilophyllum* fronds with the type of inflorescence now known under the generic name of *Williamsonia*.

Zamites (Williamsonia) gigas, Lindl. & Hutt.

There have yet been found few examples of this species from which good cuticular preparations can be made. One specimen, however, from Marske, which has large pinnæ and apparently belongs to this species, yields preparations which show the cells of the upper epidermis fairly clearly. The lower epidermis is somewhat crumpled, and the preparations made from it are always rather dirty; its cells are very indistinct, and the pits in which the stomata appear to have been sunk are usually filled with matrix. We can, however, make out some of its epidermal characters. The upper epidermis is thinly cuticularised, and is composed of cells of the usual type with very sinuous outlines. The lower cuticle is also very thin, and the outlines of the cells cannot be seen. The stomata are arranged in fairly regular rows with their axes at right angles to the rows; the guard-cells appear to be considerably sunken and are surrounded by a brown, rather highly cuticularised area, probably the walls of the pit. The guard-cells possess

* Seward (1912), p. 108, pl. 12. figs. 40–42 & 45.

the same characteristic thickenings as previously described; the crescentic patches are terminated in sharp points (*cf.* text-fig. 31) and partially cover the ventral patches, while the central space on either side of the slit is thinner. The small projection from the centre of the crescentic patch which is characteristically seen in *Ptilophyllum pecten*, *Dictyozamites*, etc., is here apparently absent.

A large frond from Marske with a form somewhat like that of *Zamites gigas* yielded, after some difficulty, a cuticular preparation of the upper epidermis, in which the cells are rounded in shape and quite distinct from the other examples in the present group.

Zamites (?) sp. Scale-leaves from stem.

In the Natural History Museum (Palæobotanical Department) of Stockholm, there is an interesting specimen, collected at Whitby by Prof. Nathorst in 1909. It appears to be the remains of a branching stem about 5 cm. wide; one part of it is fairly weil preserved, and seems as if covered with numerous overlapping scales or leaves; it is

Fig. 31.

Stoma of *Zamites gigas*, Lindl. & Hutt., showing form of the thickening on the upper side of the guard-cells. The circle surrounding the stoma represents the outline of the shallow pit in which the stoma was sunk.

somewhat similar to those of the James Yates Collection, figured by Wieland (1911, figs. 2, 3).

The scale-leaves appear as if lanceolate in shape, of rather thick texture, and striated; they are very indistinctly outlined. They yield, however, cuticular preparations which show a certain amount of structure, though considerably obscured by a mass of hypodermal or other tissue, which was evidently thick-walled and has resisted both decay and maceration. The actual epidermal cells are not clearly seen, but some of the stomata are quite visible; they appear to be similar in both form and arrangement to those previously described (see Pl. 19. fig. 2).

Otozamites graphicus (Leckenby, ex Bean MS.) n. comb.

Fronds of this form from Marske yield good preparations, but the cuticles are very thin and fragile, and hence only small pieces are obtainable. The similarity of its cuticular structure to that of the foregoing types is very noticeable. The upper epidermis has small squarish cells with rather thick walls showing closely approximated folds. The lower cuticle is very thin, with the usual type of cells; the stomata are rather sparsely scattered, only 40–50 per sq. mm. occurring in the specimens examined. In this they contrast with *Otozamites Feistmanteli* from the same bed, in which the stomata are twice as numerous. The stomata are arranged more or less in lines between the veins which are marked by the greater elongation of the epidermal cells; they have a fairly regular orientation, the pore being at right angles to the veins. They are not deeply sunken.

The stomatal structure (see Pl. **19.** fig. 4) is like that of *Zamites*. The thickening patches are hemispherical to spindle-shaped, and the central area is thin. The sides of the pore seem to be slightly thickened, and the two lateral subsidiary cells are also somewhat thicker than the other epidermal cells.

Otozamites Feistmanteli, Zigno.

The dark shale bed at Marske has yielded good specimens of the smaller *Otozamites*, which gives good cuticular preparations. These show some interesting points; the stomata are clearly seen and are very numerous, being almost contiguous in lines between the nerves. About 100 occur in each square millimetre. In structure and form they are similar to the stomata of the larger species, but the lateral thickening patches thin out gradually towards the slit, showing no sharp margin, but more or less merging in towards the central area. The latter is very slightly cuticularised except at the edges of the pore, which stands out clearly as a dark central line (*cf.* Pl. **19.** fig. 3). The subsidiary cells are again slightly thickened, and their relations to the other epidermal cells are often well seen.

Dictyozamites Hawelli, Seward.

The cuticular structure of *Dictyozamites Johnstrupi*, Nath. has already been described in some detail by Prof. Nathorst (1907, p. 12, Taf. 3. figs. 2–8). The structure of the present examples from Marske does not differ materially from that of the Bornholm examples, but the structure of the stomata can now be further elucidated. As in the former cases, the upper epidermis is devoid of stomata, and is composed of cells with very sinuous walls, the reticular course of the veins being marked by the elongation, narrowing, and thickening of the cells above them. The folds in the cell-walls of this species are not so deep as those previously described. The lower epidermis is less strongly cuticularised than the upper; the course of the veins is again marked by elongated cells with less folded walls. The stomata occur only between the veins; they are more or less irregularly scattered, but still show a distinct tendency to have the pore

placed at right angles to the adjacent veins. The stomata are numerous, about 120 per sq. mm. Small papillæ occur on many of the epidermal cells, but are not so conspicuous as in *D. Johnstrupi.* The structure of the stomata appears somewhat complicated owing to the presence of what seem like small thickened outgrowths or papillæ from the surface above the guard-cells, and which are shown in Pl. **19.** fig. 8, where the guard-cells have been by some means pulled apart. In other cases they appear to overlap the central space, as shown in Pl. **19.** fig. 6, and Pl. **20.** fig. 7, or give the impression of the guard-cells interlocking with each other, as mentioned by Prof. Nathorst. These projections are probably of a nature very similar to those observed in the case of *Ptilophyllum pecten* (*cf.* Pl. **19.** fig. 1). Sometimes they are not visible (*cf.* Pl. **19.** fig. 7), being probably on the under side of the preparation; in this case the thickening patches are very comparable to those in *Otozamites.* On either side of each stoma are subsidiary cells, somewhat thickened and often much elongated (*cf.* Pl. **19.** figs. 6–8). In preparations mounted with the lower side of the stomata uppermost, the latter seem to have the same form as in several other examples of this group, the ventral patches on the guard-cells being somewhat thinner.

Anomozamites (Wielandiella) Nilssoni (Phill.), n. comb.

Leaves of an *Anomozamites* form have been found in Yorkshire near Gristhorpe, Marske, and Roseberry Topping. They are very similar in shape to those of *Wielandiella angustifolia,* Nath., and may well have belonged to plants bearing floral structures similar to those found by Nathorst in connection with his species; such structures are not, however, yet known with certainty from England, though stems have been found which are almost identical with those of the Rhætic plant. The cuticular preparations obtainable from the Yorkshire *Anomozamites* leaves are exceedingly beautiful, and show clearly the epidermal and stomatal characters. The leaves from the Lower Estuarine Series at Marske differ slightly from those of Gristhorpe in the possession of numerous spherical papillæ on their lower cuticles; the stomata are also slightly smaller.

In the specimens studied the upper epidermis is very uniform, and is composed of more or less rectangular cells; the courses of the veins are not clearly marked off, but occasionally they are indicated by lines of slightly more elongated cells. The cell-walls are again sinuous or zig-zag, but the folds have a different form from those in the other genera, each of the ridges and grooves being angular rather than nail-shaped or rounded; each point appears to possess a small pad of cutin. The upper epidermis is devoid of stomata. In some preparations the cuticle from the rachis of the frond is also seen; this has regular rectangular cells with straight walls, and occasional structures like rudimentary stomata. The lower epidermis has a structure similar to that of the upper, but the cells are less regular, and the stomata are irregularly scattered (*cf.* Pl. **20.** fig. 8). The courses of the veins are seen, though not very clearly, and no stomata lie upon them. There are about 70 stomata per sq. mm., and their form is very clearly seen in most examples. It is shown in Pl. **19.** fig. 5, and Pl. **20.** fig. 8. The central slit is

bordered by two fine linear membranes, beyond which are the thickening patches somewhat hemispherical in shape, with a straight inner surface and rounded or pointed ends. The inner surface of each appears to be carried on as a wall, a fact which is of some importance in the interpretation of the structure. There are two crescentic subsidiary cells.

In their structure these stomata resemble the examples seen in *Otozamites*, especially *O. graphicus*, and also in *Tæniopteris vittata* (*cf.* Pl. 19. fig. 12).

Tæniopteris vittata, Brongn.

The entire linear-lanceolate fronds with a strong petiole, central midrib, and dichotomising nervation which are so common in the Yorkshire plant-beds were designated *Tæniopteris vittata* by Brongniart and, as the name implies, regarded as fronds or pinnæ of a fern. Phillips in 1829 (p. 147) regarded it as allied to the recent *Scolopendrium*, but subsequent authors * have for the most part considered it to be allied to *Marattiopsis* and have placed it among the Marattiales. Another view was that it had affinities with the modern genus *Oleandra*, since it possessed a petiole with a clean-cut base, which suggested that it had become detached from its original stem or rhizome by the formation of an absciss-layer †; thus the generic name of *Oleandridium* was used by Schimper (*loc. cit.*), Feistmantel, and others.

On the other hand, the view was put forward by some authors, especially Bornemann (1856, p. 59), that it was really the pinna of a pinnate Cycadean frond such as *Stangeria*, and the name *Stangerites* was instituted to replace *Tæniopteris*. Several subsequent authors have kept in mind this possibility, but no definite evidence has been forthcoming in support of either view. *T. vittata* has never been found bearing synangia or sporangia; it has also never been found attached as a pinna to a larger frond. Recently, however, it has been found in association with Cycadean stems of the *Wielandiella* type, and one specimen appears to show organic connection between a frond and one of these stems. It is almost certain that we have to deal with entire fronds and not with pinnæ, and thus a very close comparison is offered with the fronds of *Anomozamites* (*Wielandiella*); the latter possess the forking nervation of *Tæniopteris* and may be regarded as segmented fronds of the *Tæniopteris* type. *T. vittata* itself is sometimes found with the lamina divided into irregular segments. When we come to examine the cuticular structure we obtain very strong confirmation of the Cycadean view.

In its cuticular structure *Tæniopteris vittata* approaches very closely to *Anomozamites Nilssoni*. The upper epidermis is fairly strongly thickened and was composed of squarish to hexagonal cells, with somewhat sinuous walls (Pl. 20. fig. 5). The vein-courses are only slightly differentiated, the cells being more regularly arranged in rows. The outline of the cell-walls is interesting owing to the presence of a solid piece of thickening at the point of every fold (this is just visible in the photograph); in some cases it gives the appearance of an almost straight wall ornamented with projecting

* Schimper (1869), p. 607.

† Seward (1900), p. 158.

tooth-like masses of thickening, but it can always be referred to the same general type of wall-folding. We see the same tendency in *Anomozamites*. The lower epidermis is composed of cells similar to those of the upper epidermis, but of a somewhat larger size; their walls are thinner and may be sinuous or have the folds filled in, as just mentioned. A few rounded hair-scars are present. The stomata are absent from the nerve-courses and are irregularly scattered between (*cf.* Pl. **20**. fig. 6); about 60–70 occur in each square millimetre. They have the same general form as previously described, but are apparently rather more complex. Some of the examples from Marske (Pl. **19**. fig. 12) do not differ greatly from the *Anomozamites* stomata except in the proportions of thickening, the areas abutting immediately on the slit being the more strongly thickened. The stomata in the Gristhorpe examples appear to have been slightly sunken; in most cases the pore is clearly seen and is surrounded by a strongly thickened margin running to a point at either pole (Pl. **19**. fig. 11). The outer (upper) thickening patches are often not so clearly defined as in the other genera, but have the same relations to the auxiliary cells as those of *Anomozamites*. These outer patches are often thinner than the inner ones and occasionally appear to project into the centre, almost above the slit (Pl. **19**. fig. 10); they sometimes develop a small projecting hump, similar to that seen in *Ptilophyllum pecten* and *Dictyozamites*. Though it is very difficult now to understand what the structures, which we see in the surface view, must have meant in the solid, yet it is quite evident by comparison with the cuticles of other groups, that *Tæniopteris vittata* possessed essentially the same epidermal and stomatal characters as the other fronds in the Bennettitalean group, being especially like *Anomozamites*.

When this is considered in addition to the facts quoted above, it seems that we have strong reasons for removing this species and its near allies from among the ferns and for including it in the Bennettitales.

Tæniopteris major, Lindl. & Hutt.

Some *Tæniopteris* fronds occur at Gristhorpe which are somewhat larger than those of *T. vittata*, but are readily distinguishable by their distinct and widely separated dichotomising veins, which are one millimetre apart or more and are very characteristic; these fronds are probably distinct from *T. vittata*, and may be referable to the form described by Lindley and Hutton as *T. major*.

In its cuticular characters it does not differ much from the species just described; the cells of the upper epidermis are rather large and have well-developed angularly folded walls, slight additional thickenings being present on the tips. The lower epidermis has somewhat scattered stomata which resemble very closely those of *T. vittata* (Pl. **19**. fig. 9).

In this case the epidermal characters do not, so far as we have seen, present any sharply marked features on which we can rely for the separation of the related forms *major* and *vittata*.

II. Nilssoniales.*

Nilssonia, Brongn.

While the cuticles of the genera already described show a very considerable agreement, both in the structure of their epidermal cells, and also in the form and arrangement of the stomata, the cuticles of the remaining genera *Nilssonia*, *Ctenis*, and *Ptilozamites* are quite distinct from them. In these forms the epidermal cells are somewhat irregular in shape, being rounded, hexagonal, or rectangular; the walls are straight without any indication of folding. The stomata appear to be somewhat sunken, and when any trace of the guard-cells can be seen, they apparently lack special thickening and have a more or less rounded contour. The appearance of these cuticles therefore marks them at once as distinct from those of the Bennettitalean group.

The Nilssonias must have been important constituents of the Jurassic vegetation of the Yorkshire area. Fronds of *Nilssonia compta* occur abundantly in the Middle Estuarine bed in the neighbourhood of Gristhorpe Bay. In the same locality *N. mediana* occurs; this is almost identical in form with a plant which is very abundant in the Lower Estuarine beds of Marske and Roseberry Topping, but which possesses very much more delicate cuticles. The same form occurs at Whitby, while another type, closely allied to *N. compta*, but probably a species new to England, is found at Roseberry Topping. The cuticles of these three species or forms have been examined, and their characters are briefly described below. The cuticles of the Swedish species *brevis*, *polymorpha*, and *pterophylloides* have been described and figured by Prof. Nathorst. They apparently agree somewhat closely with the English species described here, though little or nothing could be made out about the form of their stomata.

Nilssonia compta, Phill.

The examples of this species from the Gristhorpe bed indicate that they originally had a somewhat delicate texture, and owing to this and to the thinness of the cuticles it is not easy to obtain good cuticular preparations from them. Even after portions of the carbonised lamina have been successfully removed from the matrix they frequently break up into numerous small fragments during the clearing process. It is believed that this affords a character of real value in describing and identifying fronds. In many descriptions of leaf-impressions, the lamina is described as leathery or coriaceous, from the appearance of the specimen when still attached to the rock or even from the appearance of its cast; in most of these cases little value can be assigned to such a statement. When, however, we are able to remove the carbonised or mummified plant from the matrix and investigate the structure of its cuticle, we have definite grounds for a statement as to the comparative texture of the lamina.

In the case of the plants preserved in the fine-grained mudstone of the Gristhorpe bed, we can say with some confidence that such fronds as *Tæniopteris vittata*, *T. major*, *Ctenis falcata*, and especially *Ptilozamites Leckenbyi*, had a firm and coriaceous lamina. Others, such as *Anomozamites Nilssoni* and *Nilssonia compta*, were of intermediate

* See page 196.

character, while *Nilssonia mediana* and *N. orientalis* had a distinctly delicate or thin lamina, approaching the type possessed by the ferns and seldom separating from the matrix in an entire condition.

The upper epidermis of *N. compta* is very distinct from the lower. It possesses small rather irregularly-shaped cells arranged, to some extent, in rows. The individual cells vary greatly in shape; they may be isodiametric with rounded or angular outlines, or they may be more elongated, and of rectangular to fusiform shapes. The latter kind probably occur above the nerves. All the cell-walls are straight and not sinuous. There are usually no stomata present, but in one or two cases, structures which may be stomata, are seen near the margin of the lamina. A few rounded papillæ occur, these being of the type common to most of the Nilssonias. Their form is better seen on the rachis and in other species.

The cells of the lower epidermis are much more clearly seen; the nerve-courses are distinctly marked by the occurrence of rows of elongated cells, often bearing papillæ, but devoid of stomata. The spaces between the nerves are occupied by rounded cells, with a good deal of thickening in the corners. The cells surrounding the stomatal apertures are much thickened. The stomata on these leaves are not numerous; estimates from the very fragmentary cuticles indicate between 40 and 50 in each sq. mm. It is almost impossible to make out the exact structure of the stomatal openings, but the following features are recognisable. Each aperture is surrounded by crushed thickened cells, which evidently formed, in their original condition, a chimney-like structure, being raised beyond the surface of the leaf, and enclosing a pit, at the base of which the guard-cells were placed. Amongst recent Cycadean cuticles, a similar condition is seen in *Dioon* and in *Cycas revoluta*. The fossil cuticles do not show the projection of the cells surrounding the stomatal apertures, owing to crushing in preservation. The cells are seven or eight in number, and often show a star-like arrangement. Their relations to the ordinary epidermal cells are not clear. When some of the preparations are mounted so that their inner side (viz., that abutting on the mesophyll) is uppermost, the remains of the guard-cells can often be distinguished (Pl. 19. figs. 14 & 18). The guard-cells themselves may be somewhat indefinite, but the pore is usually quite distinct. The thickening of the guard-cells seems to be of a simple type, and not complex as in the Bennettitalean fronds; this may perhaps be correlated with their sunken position.

The cuticle from the rachis below the frond presents some distinctive features. It is composed of elongated spindle-shaped cells, giving the appearance which sclerenchymatous cells show in longitudinal section. At frequent intervals occur oval cells, which are considerably more cuticularised than the rest. In the centre of each of these is a rounded area, probably representing a short papilla. Structures of this nature are also found sparingly on both surfaces of the lamina, as mentioned above.

Nilssonia mediana (Leckenby, ex Bean MS.), n. comb.

Examples of this species from Gristhorpe do not yield good preparations owing to the delicate nature of the cuticle; specimens from Marske, which are very similar in external form, have a well-thickened cuticle, and preparations from these show the outlines of

the cells very clearly. The cuticles of *N. mediana* differ from those of *N. compta* only in detail. The cells of the upper epidermis are more elongated and spindle-shaped, and those of the lower epidermis are very sharply differentiated according to their position above or between the nerve-courses (Pl. **20.** fig. 10). Some papillæ are present, and each of the rounded cells from the areas between the nerves is thickened externally and forms in consequence a slight convex projection on the surface of the cuticle. The stomata can be more clearly seen than in *N. compta.* The cells surrounding the stomatal aperture are only slightly raised and thickened, and therefore they are less crushed. The raised portions are in this species seen to be merely small outgrowths from the ordinary epidermal cells, slightly thickened (*cf.* Pl. **19.** fig. 15).

Nilssonia sp.

A new form of *Nilssonia* has recently been discovered at Roseberry Topping, Yorkshire. It is closely allied to *N. compta* of the Middle Estuarine beds, but has more rounded and less regular leaf-segments, approaching the *N. polymorpha* type. It also has a very marked wrinkling of the lamina. It yields good cuticular preparations (Pl. **20.** fig. 9), though these are somewhat brittle. The stomatal apertures in this species are surrounded by several strongly thickened conical cells which originally must have formed conspicuous projections, but which are now usually much crushed (see Pl. **19.** fig. 13). The papillate hairs are also well marked in this new form.

Nilssonia orientalis, Heer.

Of the three species of *Nilssonia* described in Prof. Seward's 'Jurassic Flora of Yorkshire,' *N. compta* and *N. mediana* were well defined and represented by many specimens in the then existing collections, while the third was only known from a few examples. The name given to this was *N. tenuinervis*, a title which had originally been proposed by Nathorst (1880, p. 35) for linear fronds, little divided and having numerous fine veins. It now seems impossible to separate this English form from the Siberian type described by Heer (1878, Pl. 4. figs. 4–9) as *N. orientalis* *. In his original MS. notes on the specimens amongst which *N. tenuinervis* was found, Prof. Nathorst † remarked on the great similarity in external form between the new species and some examples of *Tæniopteris vittata*; and, in fact, they can only be distinguished readily in well-preserved examples. In 1909, when working at the revision of the Swedish species of *Nilssonia* and studying their epidermal characters, Prof. Nathorst (1909, p. 27) made cuticular preparations of some fronds from Cloughton Wyke, Yorkshire, which were in his collection. These preparations showed a type of structure unlike that of the other Nilssonias, and identical with that described above for *Tæniopteris vittata.* Nathorst concluded that the Yorkshire frond was not a true *Nilssonia,* but was rather allied to the ferns; he accordingly instituted the new genus *Nilssoniopteris*, giving as

* With reference to the nomenclature of this form see Thomas (1913), p. 240.

† Our best thanks are due to Prof. Nathorst for the kind way in which he placed all his material at my disposal, for showing me many of his manuscript notes and adding materially to the elucidation of this difficult species.—H. H. T.

its characters the distinct cuticular structure and the dichotomising of some of the secondary veins. In 1911, while working in Prof. Nathorst's laboratory, one of us was able to re-examine his specimens and preparations, and found that one of Prof. Nathorst's fronds, that figured on Pl. 6. figs. 23 & 25, was really a specimen of *Tæniopteris vittata*, showing a forking venation. As this form yields good preparations it had been used in the description of the examples figured on his Pl. 7. fig. 21.

From the other specimen only very fragmentary preparations could be obtained, but they were sufficient to show that their structure was quite distinct, agreeing with that of true Nilssonias, in which the cuticles are extremely delicate. In this form the fragments of cuticle (one of them is shown in Pl. 20. fig. 11) show that the upper epidermis is composed of elongated rectangular or tapering cells, with straight walls similar to those of *N. mediana*. The lower epidermis has fine rectangular or squarish cells with straight walls and small dark rounded structures like the papillate hairs of *N. compta* and *N. mediana*. No stomata can be clearly seen.

Other examples of the same kind have been obtained from the Gristhorpe bed; they agree in the characters given above, but do not add any information. They show a well-marked minute wrinkling of the cuticular film which rather obscures detail.

From these facts it appears that the name *Nilssoniopteris* must be abandoned, for the cuticles of the Yorkshire specimens referable to *Nilssonia orientalis* (*tenuinervis*) are of the same type as those of other species of *Nilssonia*.

Ctenis falcata, Lindl. & Hutt.

Specimens of this species found in the Gristhorpe bed flake off very readily from the matrix and yield fairly good cuticular preparations.

The upper epidermis is very strongly cuticularised, and the thickening evidently originally extended down the radial walls to a considerable extent, for the cell outlines are now represented by thick badly defined lines of cuticle. The cells above the nerves are especially strongly cuticularised, often causing the nerve-courses to stand out as dark, slightly raised lines; only two or three rows of cells, however, are affected, and not a broad series. The anastomosing of the veins is clearly shown on both the upper and the lower cuticles. The cells of the upper cuticle are irregular in outline, but are more or less isodiametric, varying between squares and hexagons. Some of them seem slightly papillate, but are not markedly so. No stomata are present on the upper surface. The lower cuticle (Pl. 20. fig. 13) is somewhat similar to the upper in thickness, but the cell outlines are larger and more distinct. The vein-courses are marked by a more regular arrangement of cells, and the stomata occur somewhat scattered in the intervening areas. Their numerical distribution is from 60–70 per square mm.

As in *Nilssonia*, the guard-cells are sunk and are not clearly seen. The cells surrounding the stomata-openings are not much differentiated in form or thickening from the ordinary epidermal cells; where they adjoin the guard-cells, however, there is a solid ring of thickening round the stomatal cavity (Pl. 19. fig. 19). The latter is apparently not very deep, and the guard-cells are often seen at its base. They are

slightly thickened, and in many cases are not preserved, but the stomatal slit is frequently visible.

Ctenis falcata presents a type of stomatal structure comparable with that seen in *Nilssonia mediana*. In the former species, however, there is little or no tendency towards the papillate outgrowths from the subsidiary cells surrounding the stomatal apertures, which is so pronounced a feature in some Nilssonias, for example *N. compta*.

PTILOZAMITES (CTENOZAMITES) LECKENBYI (Leckenby, ex Bean MS.), n. comb.

The cuticles of this form have already been figured by Prof. Nathorst (1908, Taf. 1. figs. 3–5) as providing an example of a frond with stomata on one side of the pinnæ only. He did not enter into a detailed description of the structures seen.

In comparing the structure of the cuticle with that of other genera, the following points may be noted. The leaves have a very stout texture with thick cuticles so that the leaflets separate off whole from the matrix and can be easily handled. In most of the specimens examined the serration of the margin is not pronounced, but a few teeth are seen near the apex. The upper cuticle is very thick and shows very clearly the outlines of the epidermal cells which must originally have had their radial walls very considerably cuticularised. The cells are irregularly shaped, but are straight-walled and somewhat rectangular. The cells above the nerves are more elongated than the rest. The lower cuticle is also thick and shows cells similar in form to those of the upper epidermis. The cells are slightly elongated above the veins, but the courses of the latter are not clearly defined and are not always devoid of stomata. The stomata were numerous, their distribution being about 90 per square mm. (Pl. **20**. fig. 12). In form they show considerable resemblance to those in *Ctenis*, being slightly sunk, and having the walls and opening of the stomatal cavity much thickened (Pl. **19**. fig. **17**); the cuticle round the opening, in fact, forms a little ring, slightly raised beyond the surface of the pinna. The seven or eight subsidiary cells are somewhat thickened and appear as a group darker than the rest. On mounting a lower cuticle so that the mesophyll side is uppermost, the outlines of the guard-cells are faintly seen; these appear to have some resemblance to those of the Williamsonia-Tæniopteris group. The slit lies at right angles to the longer diameter of the stomatal cavity, and on either side of it there are distinct though faint indications of guard-cells (?) with pointed ends (Pl. **19**. fig. 16).

(*c*) The Cuticles of some other Types of Fossil Cycadean Fronds.

The cuticular structure of some other genera have been described by other authors, but in several cases the figures given are not sufficiently detailed or accurate to allow of their close comparison with the examples here described. Prof. Nathorst has figured and described the cuticles of two species of *Pseudocycas* from the Lower Cretaceous (1907, pp. 7, 9, Taf. 2. figs. 1–11). These cuticles show more or less rectangular cells arranged in regular rows and having undulating walls. The stomata are not clearly recognisable, but from Taf. 2. fig. 11, they appear to be somewhat similar in general

character to those of *Anomozamites* and the Bennettitalean group. Nathorst compares the structure of these forms with those of *Otozamites*, *Pterophyllum*, &c., and it does indeed seem probable that these *Pseudocycas* fronds should be included in the Bennettitalean group, though in the disposition of the stomata in a furrow they are distinct from any of the known Jurassic forms.

Berry, in his account of the Lower Cretaceous flora of Maryland (1911, p. 334), gives a diagrammatic figure of the cuticle of *Dioonites* (= *Zamites*) *Buchianus*, Ett. The cells as in *Pseudocycas* are arranged in regular rows. They are rectangular and had somewhat undulating walls. The stomata are all orientated in the same direction (cf. *Ptilophyllum*, &c.), presumably with their long axes parallel with the long axis of the pinna. If the analogy with *Ptilophyllum* held, however, the stomata should be orientated at right angles to the long axis of the pinna. The structure of the guard-cells is shown diagrammatically and cannot therefore be strictly compared with our types; there is considerable probability, however, that they are similar in form to those of *Otozamites* and *Tæniopteris*. Schenck has figured *Dioonites Dunkerianus* with sinuous walls and stomata irregularly scattered. We can probably, therefore, include *Zamites* (*Dioonites*) in the Bennettitalean group.

The cuticular structure of various species of *Thinnfeldia* has been described by Schenk, Seward, Gothan, Zeiller, and other authors. It is very doubtful, however, whether this genus should be included among the Cycadophyta. The cuticular structure seems to be distinct from that described above, and is apparently more closely related to that of the Ginkgoales, especially so far as the stomatal form is concerned. There is an approach to the structure shown by *Nilssonia mediana*, but on the whole *Thinnfeldia* seems to be quite distinct.

(*d*) Summary of the Structure of the Fossil Cuticles.

The comparison of the structures just described brings out very clearly one point, viz., that the Cycad-like fronds from the Jurassic rocks of Yorkshire fall into two sharply divided groups according to their epidermal structure. The fronds in the first group have epidermal cells with sinuous walls and comparatively thin cuticles; the cells are in general rectangular in shape, but in most cases their shape is not very apparent. The stomata occur only on the lower side of the leaf and are usually absent below the vein-courses; they exhibit a strong tendency towards arrangement with their axes at right angles to the veins. Though there is some variation in the details of stomatal structure, the general plan is as follows. The guard-cells were level with the surface or only slightly sunk; the outlines of the guard-cells themselves are never seen but only those of the thickenings which they possessed. The thickenings of the guard-cells usually appear as lamellæ of definite shape and give the stomata a characteristic appearance; on either side of the pore is a pair of smaller patches, probably representing the lamella from the lower side of the guard-cells, and outside there is another pair of lamellæ, usually somewhat hemispherical in shape, representing the thickenings from the upper side of the guard-cells. At the poles there are usually two clear spaces,

looking sometimes like cells, but probably representing the thin places above the ends of the guard-cells. More or less surrounding the stomata at the sides are two large subsidiary cells, often somewhat thickened. The above description applies both to (*a*) pinnate compound fronds, e. g. *Ptilophyllum*, *Otozamites*, *Dictyozamites*, and *Zamites*, some of which are known to have belonged to plants bearing flowers of the *Williamsonia* type, and to (*b*) simple fronds, e. g. *Tæniopteris*, which is usually entire, and *Anomozamites*, which is usually pinnately lobed. Fronds of the latter have been found to belong to plants with a peculiar type of Bennettitalean flower (*Wielandiella*). There are then, strong grounds for regarding the type of cuticular structure described above as characteristic of the fronds of the Bennettitales.

The cuticles of the second series, which includes the genera *Nilssonia*, *Ctenis*, and *Ptilozamites*, are sharply marked off from those described above. In this section the cuticles may be thin (as in the Nilssonias) or very thick; they appear to have been formed from cells of elongated, rectangular, rounded, or fusiform shapes, with straight walls. The stomata are on the under side of the leaves and exhibit no regular arrangement, the guard-cells are somewhat deeply sunken, and the six or eight thickened subsidiary cells which surround them often form a somewhat overarching canopy. The guard-cells are hemispherical or spindle-shaped, they are only thinly cuticularised, and definite lamellar thickenings are seldom seen.

The cuticles in this group do not agree with one another so closely as do those in the Bennettitalean group, *Ctenis* and *Ptilozamites* are similar, but the *Nilssonias* are not so closely related. The fronds were variously shaped, those of *Ctenis* and of some species of *Nilssonia* were large and pinnate, *Ptilozamites* was bipinnate, while the fronds of *Nilssonia orientalis* were simple and often entire or only slightly lobed. It may be noticed that the thickness of the cuticle in these forms bears an apparently definite relation to the size of the frond. Of the bipinnate *Ptilozamites* no complete fronds have been obtained, but they were probably of considerable size, their cuticles were very thick; the large fronds of *Ctenis*, and also of the Lower Estuarine form of *Nilssonia mediana* had cuticles of considerable thickness. The smaller fronds of *Nilssonia compta* from Gristhorpe had thinner cuticles, while the much smaller entire fronds of *Nilssonia orientalis* had very delicate cuticles. We see no such gradation among the Bennettitalean group. We know very little about the affinities of the plants which bore the fronds placed in this second section. Prof. Nathorst has found fronds of *Nilssonia pterophylloides* associated with numerous seed-like bodies in such a way as to render their original connection probable, but the stems and reproductive organs of the other species and genera are as yet quite unknown. Though it is quite possible that some of these plants were closely related to the recent Cycadales, there is as yet no definite evidence in support of this view. It may be convenient if we institute the name of NILSSONIALES for the group of fronds which has just been described.

IV. COMPARISON OF RECENT AND FOSSIL CUTICLES.

The difficulty of comparing the epidermal structure of the recent and fossil fronds is considerable owing to the impossibility of obtaining good sections through the latter. It is, therefore, necessary in most cases to employ only the information obtained from surface view, and since in most cases the different types of stomata are chiefly to be distinguished by their appearance in transverse section, our work becomes much more difficult. It is possible, however, to notice a number of points of resemblance, and in fact many interesting comparisons can be made.

In the first place we may notice that the fossil fronds, like the modern ones, exhibit some xerophytic tendencies in the thickness of their cuticles, in the frequently sunken stomata, and in the very small number of stomata per square millimetre, the numerical distribution of stomata in both being remarkably similar. These facts may indicate that the xerophytic characters of the modern Cycadean fronds are ancestral.

Comparisons can be drawn between the shape and structure of the guard-cells. The sections through stomata of *Bennettites Morierei* figured by Lignier, indicate that the Bennettitalean stomata had a structure of the general Gymnosperm type, and that the guard-cells showed the characteristic Cycadean form. The appearance in surface view of the guard-cells of several genera, when they are not obscured by overlying cells, is somewhat characteristic. It is well seen in *Stangeria*, *Bowenia*, and sometimes in *Zamia*, *Macrozamia*, and *Encephalartos*. The guard-cells are thickened in a peculiar way with a small oval thin patch round the pore, on either side of which is a spindle-shaped or crescentic thickened mass. There is a thin patch above each end of the guard-cells, but a solid or Y-shaped thickening at the points of contact of the guard-cells. The resulting shape, which may be seen from the figures, seems to be fairly constant for all modern Cycads, and is very characteristic, being modified in the case of the deeply sunken forms. The same type of stoma is seen in most of the fossil fronds examined.

The Bennettitalean stomata possessed guard-cells with very peculiar thickenings, but which are referable to the same general type as exhibited by the modern fronds. We had a central thin region round the pore and two fusiform or crescentic patches on either side (compare the figures of *Zamites*, Pl. 19. fig. 2, and *Otozamites*, Pl. 19. fig. 3, with figures of *Zamia*, text-fig. 21, and *Stangeria*, Pl. 17. fig. 1).

We have to remember, however, that in looking at the recent stomata the most noticeable thickening is due to the lignification of the guard-cells, while in the fossil forms presumably nothing but cutin remains. In order to get preparations of the recent structures which are really comparable with the fossils, we may get rid of the woody tissue by continued boiling in Schultz's solution; in the resulting preparations little but cuticle will be left. Preparations made in this way show considerable similarity with the fossil forms (*cf.* text-fig. 32 with figures on Plate 19), the woody thickening seems to have been accompanied by a certain amount of cuticularisation which is especially seen at the poles, while on either side of the pore the thickenings on the upper surface of the guard-cells are seen as the spindle-shaped patches which

are so characteristic in the fossil forms; the thin areas between the pores and the cusp-shaped thickenings are the same as are seen in the fossil forms, especially in *Otozamites*, *Anomozamites*, and *Tæniopteris*.

The polar thickenings of the guard-cells which are seen in most of the recent forms, and which appear especially marked in *Stangeria* (where they consist of both woody tissue and cuticle), are almost entirely absent in the fossil fronds, and present a point of difference.

It is probable that the relations of the guard-cells to the surrounding epidermal cells and subsidiary cells, offer one of the most important points of comparison which can be obtained in the surface view. In the Bennettitalean fronds we have a very constant and characteristic arrangement. On either side of the guard-cells there are two large subsidiary cells of exactly the same diameter as the guard-cells and probably developed from the same mother-cell. [The small cells seen at the poles of the slit in some cases, *e. g.* in *Anomozamites*, Pl. 19. fig. 5, are probably not polar subsidiary cells but thin places above the poles of the actual guard-cells.] In the Nilssoniales group, however, and in recent fronds, the subsidiary cells are very different. They are usually six or

Fig. 32.

Stomata of *Stangeria paradoxa* as seen in surface view after prolonged maceration. Notice that the lateral upper thickenings of the guard-cells show as spindle-shaped patches, while there appear to be empty cell-like spaces at the poles. *Cf.* with figures of *Ptilophyllum* and *Otozamites* stomata.

more in number, and are arranged more or less radially round the guard-cells. In *Stangeria*, *Encephalartos*, and other forms, we find two large lateral and two smaller polar subsidiary cells, but they often become subdivided. Thus in this respect the Bennettitales are quite distinct from the recent Cycads. On the other hand the fronds included in the Nilssoniales may be closely compared with the modern forms in this character, the numerous overarching subsidiary cells of *Nilssonia*, with their strongly cuticularised points, sometimes coalescing to form a solid ring, being comparable with those of *Dioon* and *Cycas*. These overarching cells frequently are of the same type as those forming the remainder of the epidermis in both the fossil and the recent forms.

It is unfortunate that we cannot get more evidence as to the form and structure of the guard-cells in the Nilssoniales group, though in the case of the example of *Ptilozamites* figured (Pl. 19. fig. 16) the guard-cells seem to have been of somewhat the same type as those of the Bennettitales.

In comparing the general epidermal cells of the recent and fossil types we may notice that there is nothing among the modern forms which is really comparable to the very sinuous cells of *Ptilophyllum* and *Anomozamites*. The cell-walls of the *Stangeria* epidermis are somewhat sinuous, and this is of interest when taken with the forking nervation of its pinnæ, another point of comparison with the Bennettitales. If the sinuous cell-walls are to be regarded as a feature of any phylogenetic importance, it may indicate the relationships of the Bennettitales with the Pteridosperms and ferns. On the other hand, the straight walls of the Nilssonialean epidermal cells, together with the shape of the cells, are additional points of agreement with the majority of the modern Cycads.

We may summarize generally the relationship between the fossil and modern Cycadean fronds as indicated by this enquiry, as follows. The cuticular structures indicate that the Bennetittalean fronds form an easily recognizable group containing the majority of the fronds previously described as Cycadean, which are quite distinct from the modern fronds and from those of the Nilssoniales group. The latter, which includes the genera *Nilssonia*, *Ctenis*, and *Ptilozamites*, are somewhat closely allied to the modern fronds, and may probably be regarded as the true Mesozoic Cycads and the ancestors of the modern forms.

On the other hand, the Bennettitalean stomata show some important resemblances to the Cycadean ones, and may well point to a parallel line of evolution from a common stock.

It is scarcely possible at the present time to make any detailed comparison betweer the epidermal structures which have been described in this paper and those of the other groups of Gymnosperms, since in no case have the latter been studied in sufficient detail. A few general comparisons may, however, be attempted. It seems probable that of the other Gymnosperms, all of which possess guard-cells with the same characteristic pear-shaped section, the Gnetales are the most closely allied in the form of their cuticular structures. In fact, it would seem that the Bennettitalean cuticles are more closely allied to those of some of the Gnetums than to any other group, the points of comparison being the frequent arrangement of the stomata in rows, the relations of the guard-cells to the subsidiary cells, and the method of thickening of the guard-cells. In *Gnetum Gnemon* the walls of the epidermal cells are often sinuous. We have been able to examine the cuticles of *Welwitschia* and *Gnetum Gnemon*, and the stomata in these forms have also been described by Takeda* and others, but other species need to be examined before the comparison can be pressed.

The stomatal structures of *Ginkgo* † are somewhat similar to those of *Nilssonia*, but differ in the smaller and more constant shape and number of the subsidiary cells and in the very slight thickening of the guard-cells. The stomata of the Conifers ‡, while possessing guard-cells which are thickened in a somewhat similar way, seem to differ from those of the Cycadales and Bennettitales in the uniformity of the thickening and

* Takeda (1913), p. 350, text-figs. 1–5, pl. xxix. figs. 2–6.

† Seward (1911[1]), pl. v. figs. 59–62.

‡ Mahlert (1885), figs. on Taf. 1.

in the spreading out of the woody lamellæ at the poles into an almost continuous investment without the characteristic thin patches. The relations of the guard-cells to the surrounding epidermal cells also seem to be another important feature of difference.

It would seem, then, from the foregoing study, that the characters presented by the stomata and epidermal cells of the Gymnosperms can be regarded as important as indicating to some extent their relationships. In the Cycadean alliance we find some characters which have undergone comparatively little modification in the ages which have elapsed between Jurassic times and the present day, and we are consequently entitled to regard stomatal structure as being the expression of ancestral characters rather than of purely local and temporary conditions of environment. Of course, further study of other groups is needed, and we hope that it will be possible in the future to make further researches upon this line of enquiry.

In conclusion, may we express our thanks to Professor A. C. Seward for his help and advice during the course of this work, also to Professor Nathorst and other friends who have given us information and assistance.

Bibliography.

Bather, F. A. (1908).—"Nathorst's Methods of studying the cutinised portions of Fossil Plants." Geol. Mag., Dec. v. vol. v. p. 454.

Berry, E. W. (1911).—Maryland Geological Survey. Lower Cretaceous. Baltimore.

Bornemann, J. G. (1856).—"Ueber organische Reste der Lettenkohlengruppe Thüringens." Leipzig.

Chamberlain, C. J. (1912).—"Two Species of *Bowenia*." Bot. Gaz. vol. liv. p. 419.

Hill, T. G. (1912).—"Scharlach R: a Microchemical Test for Oils." New Phytologist, vol. xi. p. 72.

Karzel, R. (1908).—"Die Verholzung der Spaltöffnungen bei Cycadeen." Wiesner-Festschrift, p. 510.

Kraus, G. (1866).—"Ueber den Bau der Cycadeenfiedern." Prings. Jahrb. vol. iv. p. 305.

Lignier, O. (1894).—"Structure et Affinités du *Bennettites Morierei*, Sap. et Mar." Mém. Soc. Linnéenne de Normandie, vol. xviii. Caen.

—— (1912).—"Stomates des Écailles interséminales chez le *Bennettites Morierei* (Sap. et Mar.). Bull. Soc. Bot. de France, vol. lix. p. 425.

Lloyd, F. E. (1908).—"The Physiology of Stomata." Carnegie Institute.

Mahlert, A. (1885).—"Beiträge zur Kenntnis der Anatomie der Laubblätter der Coniferen, mit besonderer Berücksichtigung des Spaltöffnungs-Apparates." Bot. Centralbl. vol. xxiv. p. 54.

Nathorst, A. G. (1880).—"Berättelse etc." Öfvers. K. Vetensk.-Akad. Förhandl. No. 5, p. 35.

—— (1907).—"Paläobotanische Mitteilungen 1 & 2." K. Svenska Vet.-Akad. Handl. Bd. xlii. No. 5.

—— (1908).—"Paläobotanische Mitteilungen 4." K. Svenska Vet.-Akad. Handl. Bd. xliii. No. 6.

—— (1909).—"Ueber die Gattung *Nilssonia*, Brongn." K. Svenska Vet.-Akad. Handl. Bd. xliii. No. 12.

—— (1912).—"Einige paläobotanische Untersuchungsmethoden." Paläobotanische Zeitschrift, Bd. i. p. 26.

Nestler, A. (1895).—"Ein Beitrag zur Anatomie der Cycadeenfiedern." Prings. Jahrb. vol. xxvii. p. 341.

Phillips, J. (1829).—Illustrations of the Geology of Yorkshire. York.

Porsch, O. (1905).—Der Spaltöffnungsapparat im Lichte der Phylogenie. Jena.

Schenk, A. (1867).—Die fossile Flora der Grenzschichten des Keupers und Lias Frankens. Wiesbaden.

—— (1871).—Die fossile Flora der Nordwestdeutschen Wealdenformation. Cassel.

Schimper, W. P. (1869).—Traité de Paléontologie végétale. Vol. i.

Schwendener, S. (1881).—"Ueber Bau und Mechanik der Spaltöffnungen." Monatsber. d. Akad. d. Wissenschaft. Berlin.

Seward, A. C. (1900).—The Jurassic Flora. I. The Yorkshire Coast. British Museum Catalogue. London.

—— (1911[1]).—"Jurassic Plants from Chinese Dzungaria." Mém. Comité Géologique, n. s., livr. lxxv. St. Petersburg.

—— (1911[2]).—"The Jurassic Flora of Sutherland." Trans. Roy. Soc. Edin. vol. xlvii. pt. iv. no. 23.

—— (1912).—"A petrified *Williamsonia* from Scotland." Phil. Trans. ser. B. vol. cciii. p. 101.

Strasburger, E. (1867).—"Ein Beitrag zur Entwicklungsgeschichte der Spaltöffnungen." Prings. Jahrb. v. p. 297.

Takeda, H. (1913[1]).—"Some Points in the Anatomy of the Leaf of *Welwitschia mirabilis*." Annals of Botany, vol. xxviii. p. 347.

—— (1913[2]).—"Development of the Stoma in *Gnetum Gnemon*." Annals of Botany, vol. xxvii. p. 365.

Thomas, H. Hamshaw (1911).—"On the Leaves of Calamites." Phil. Trans. ser. B, vol. ccii. p. 51.

—— (1912).—"On some methods in Palæobotany." New Phytologist, vol. xi. p. 109.

—— (1913).—"The Fossil Flora of the Cleveland District of Yorkshire. I. The Flora of the Marske Quarry." Quart. Journ. Geol. Soc. vol. lxix. p. 223.

Wieland, G. R. (1911).—"On the Williamsonian Tribe." Amer. Journ. Sci. vol. xxxii. p. 433.

Zeiller, R. (1882).—"Observations sur quelques Cuticules fossiles." Ann. des Sci. Nat. sér. 6, Bot. tome xiii.

—— (1906).—Bassin houiller et permien de Blanzy et du Creusot. Fasc. 2. Flore fossile. Etudes des gîtes minéraux de la France. Paris.

EXPLANATION OF PLATES 17–20.

[The figures in Plates **17–19** were drawn with the aid of a camera lucida, the magnification being 450 diameters, unless otherwise indicated. The following abbreviations are used:—*p*, polar subsidiary cells; *l*, lateral subsidiary cells; *d*, dorsal lignified lamellæ of the guard-cells; *v*, ventral lignified lamellæ; *g*, guard-cells; *s*, stoma-opening; *i*, intercalated subsidiary cells; *a*, air-space.]

Plate 17.

Fig. 1. *Stangeria paradoxa*. Lower cuticle in surface view, showing a stoma with its characteristically thickened appearance due to the lignified lamellæ of the guard-cells. Note the radiating striæ at the poles of the stoma, due to folds in the cutin layer.

Fig. 2. The same. A hair-scar from the under side of the leaf in surface view, showing the radiating folds of the cutin.

Fig. 3. The same. Upper cuticle in surface view, showing the characteristic undulated walls of the epidermal cells and the striations due to folds in the cutin.

Fig. 4. The same. Upper cuticle in section. Note the irregular appearance of the cutin layer due to folding.

Fig. 5. The same. Lower cuticle, showing a section through a stoma. Note the position of the guard-cells, almost at the same level as the subsidiary cells.

Fig. 6. The same. Lower cuticle, showing a section through a hair-scar.

Fig. 7. *Bowenia spectabilis*, var. *serrulata*. Lower cuticle in surface view, showing a stoma; the thickened appearance is due to the lignified lamellæ of the guard-cells.

Fig. 8. The same. A stoma of the upper side of the leaf in surface view. Note the presence in this case of six subsidiary cells, two of which are polars and four laterals.

Fig. 9. The same. Lower cuticle, showing a section through a stoma. Note the position of the guard-cells with regard to the subsidiary cells.

Fig. 10. *Cycas revoluta*. Upper cuticle in section, showing the pittings of the lateral and outer walls of the epidermal cells.

Fig. 11. The same. Upper cuticle in surface view, showing the pittings of the lateral and outer walls of the epidermal cells.

Fig. 12. The same. Lower cuticle in surface view, showing the fifteen subsidiary cells surrounding a stoma-opening. The shading indicates the raising of the subsidiary cells beyond the general epidermal level (*cf.* fig. 13).

Fig. 13. The same. Lower cuticle, showing a section through a stoma. Note the presence of an intercalated series of cells between the guard and subsidiary cells, and the large air-space formed by the sinking of the guard-cells and the overarching of the subsidiary cells.

Fig. 14. *Cycas circinalis*. Lower cuticle, showing a section through a stoma. Note the sinking of the guard-cells and the absence of an intercalated series of cells (*cf.* figs. 5, 9, & 13).

Fig. 15. The same. Upper cuticle in section, showing pitting of the outer walls of the cells.

Plate 18.

Fig. 1. *Ceratozamia mexicana*. Upper cuticle in surface view, showing thin-walled and thick-walled cells. Note the layering and pitting of the thickened walls.

Fig. 2. The same. Lower cuticle in surface view, showing a stoma-opening surrounded by six subsidiary cells, two of which are polars and four laterals. The cell-walls are pitted and layered as in fig. 1.

Fig. 3. The same. Upper cuticle, showing the thick- and thin-walled cells in section.

Fig. 4. The same. Lower cuticle: a section through a stoma, showing one intercalated series of cells between the guard-cells and subsidiary cells.

Fig. 5. *Dioon edule*. Upper cuticle in surface view, showing the variation in thickness and the layering of the cell-walls.

Fig. 6. The same. A section of a stoma. Note the presence of three intercalated series of cells (i^1–i^3) between the guard-cells and the subsidiary cells; also the dorsal and ventral lignified lamellæ of the guard-cells.

Fig. 7. The same. Upper cuticle in section, showing variation in the thickness of the walls. Note the heavy cutin layer.

Fig. 8. The same. A section of the lower cuticle, showing a crystal-containing space between two epidermal cells. The space is lined and covered by cutin.

Fig. 9. The same. The lower cuticle, showing a crystal-containing space in surface view.

Fig. 10. *Encephalartos Lehmanni*. Upper cuticle in section, showing pitting of the lateral walls.

Fig. 11. *E. villosus*. Upper cuticle in surface view, showing slight pitting of the lateral walls of the cells and septation of an elongated cell at *x*.

Fig. 12. *Zamia integrifolia*. Upper cuticle in surface view, showing variation in the thickness of the walls and occasional pitting of the thin-walled cells.

Fig. 13. *Zamia muricata.* Lower cuticle, showing a stoma in section. Note the slightly sunk guard-cells.

Fig. 14. *Macrozamia cylindrica.* Section through a stoma, showing two intercalated series of cells and the long narrow air-space.

Fig. 15. The same. Upper cuticle in surface view, showing variation in the thickness of the cell-walls, also pitting and layering of the walls.

Plate 19.

[Camera lucida drawings of stomata of fossil fronds.]

Fig. 1. *Ptilophyllum pecten.* Showing the different thickenings of the guard-cells and the thin places above the poles. Specimen from Marske. × 600.

Fig. 2. *Zamites* sp. Showing outlines of stomatal thickenings. From scale-leaves on stem. Specimen in the Naturhistoriska Riksmuseum, Stockholm. × 500.

Fig. 3. *Otozamites Feistmanteli.* Stoma with differences of thickening less marked. The subsidiary cells are not thickened. Specimen from Marske. × 500.

Fig. 4. *Otozamites graphicus.* The sides of the pore appear to have been slightly cuticularised. Specimen from Marske. × 500.

Fig. 5. *Anomozamites Nilssoni.* Showing thin subsidiary cells and thin places at the poles. Specimen from Gristhorpe. × 500.

Figs. 6–8. *Dictyozamites Hawelli.* Subsidiary cells thickened: 6 and 8 show projections from upper thickenings of guard-cells. Fig. 7. Stoma seen from mesophyll side. Specimens from Marske. × 500.

Fig. 9. *Tæniopteris major.* Compare with *T. vittata.* Specimen from Gristhorpe. × 500.

Figs. 10–12. *Tæniopteris vittata.* Showing the similarity with stomata of other Bennettitalean fronds. Fig. 10 is seen from the mesophyll side. 10 and 11 from Gristhorpe, 12 from Marske. × 500.

Figs. 13, 14, 18. *Nilssonia* sp. From a specimen found at Roseberry Topping. × 500. Note in 13 the series of overarching subsidiary cells. Figs. 14 and 18 show the guard-cells as seen from the mesophyll side of the epidermis.

Fig. 15. *Nilssonia mediana.* Subsidiary cells with thickened tips overarching the guard-cells. Specimen from Marske. × 500.

Figs. 16, 17. *Ptilozamites Leckenbyi.* Stomata as seen from upper (17) and lower side (16). In the former the guard-cells can just be seen through the opening. Specimens from Gristhorpe. × 500.

Fig. 19. *Ctenis falcata.* Showing thick wall of cuticle round the stomatal cavity. Specimen from Gristhorpe. × 500.

Plate 20.

[Photomicrographs of cuticular preparations of fossil fronds.]

Fig. 1. *Ptilophyllum pecten.* Showing upper epidermis (to the right) and lower epidermis with the stomata arranged in regular rows. From Marske. × 25.

Fig. 2. *Ptilophyllum pecten.* Upper epidermis more highly magnified, showing sinuous outlines of the cells. × 170.

Fig. 3. *Ptilophyllum pecten.* Part of lower epidermis more highly magnified, showing stomata. × 200.

Fig. 4. *Ptilophyllum* sp. Showing rows of circular hair-scars with epidermal cells below. From Marske. × 200.

Fig. 5. *Tæniopteris vittata.* Part of upper epidermis, showing characteristic folded cell-walls. From Gristhorpe. × 200.

Fig. 6. *Tæniopteris vittata.* Part of lower epidermis, showing stomata which were slightly sunken, and hence the walls of the epidermal cells are out of focus. × 200.

Fig. 7. *Dictyozamites Hawelli.* Lower epidermis, showing stomata. The characteristic form of the upper thickening lamellæ is seen in a few cases. From Marske. × 180.

Fig. 8. *Anomozamites Nilssoni.* Lower epidermis with stomata. From Gristhorpe. × 200.

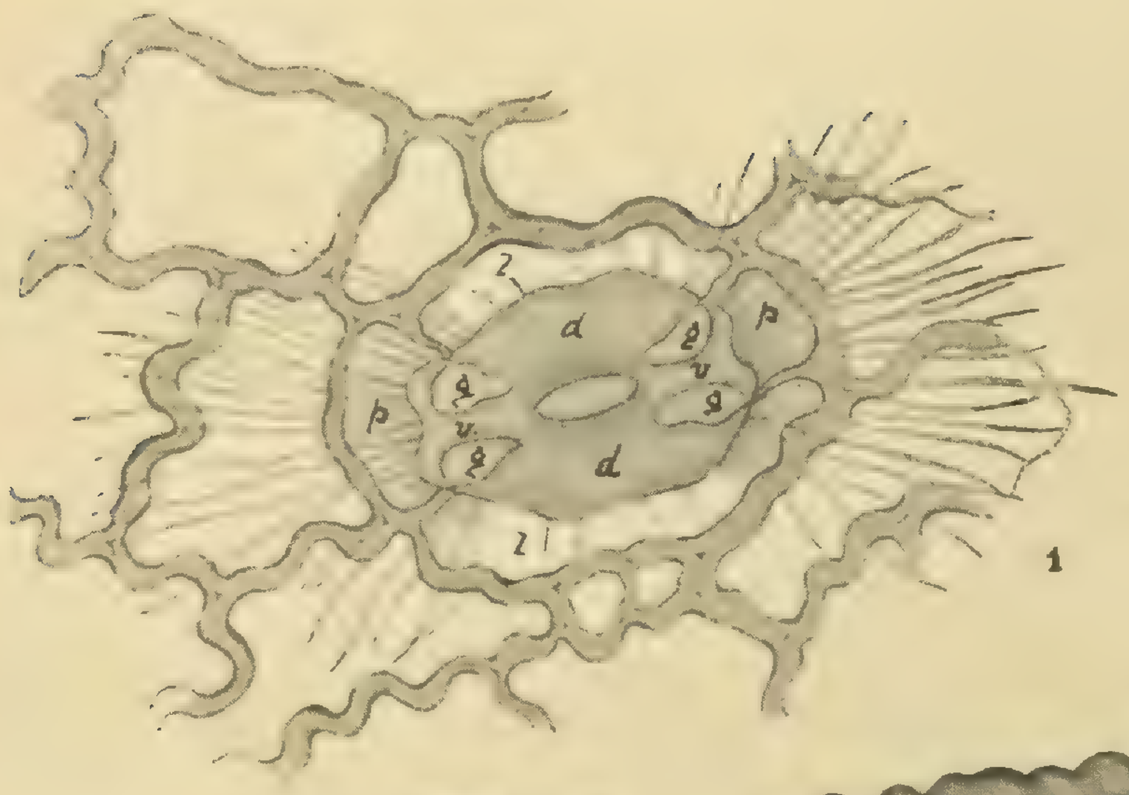
Fig. 9. *Nilssonia* sp. From Roseberry Topping. Upper epidermis, showing characteristic papillæ. × 180.

Fig. 10. *Nilssonia mediana.* Lower epidermis, showing elongated cells with papillæ occurring below the veins, while the cells of the intermediate areas are rounded. From Marske. × 200.

Fig. 11. *Nilssonia orientalis.* Portion of upper epidermis from specimen No. 323 in the Natur-historiska Riksmuseum, Stockholm. Found at Cloughton Wyke. × 200. This specimen has been figured as *Nilssoniopteris tenuinervis.*

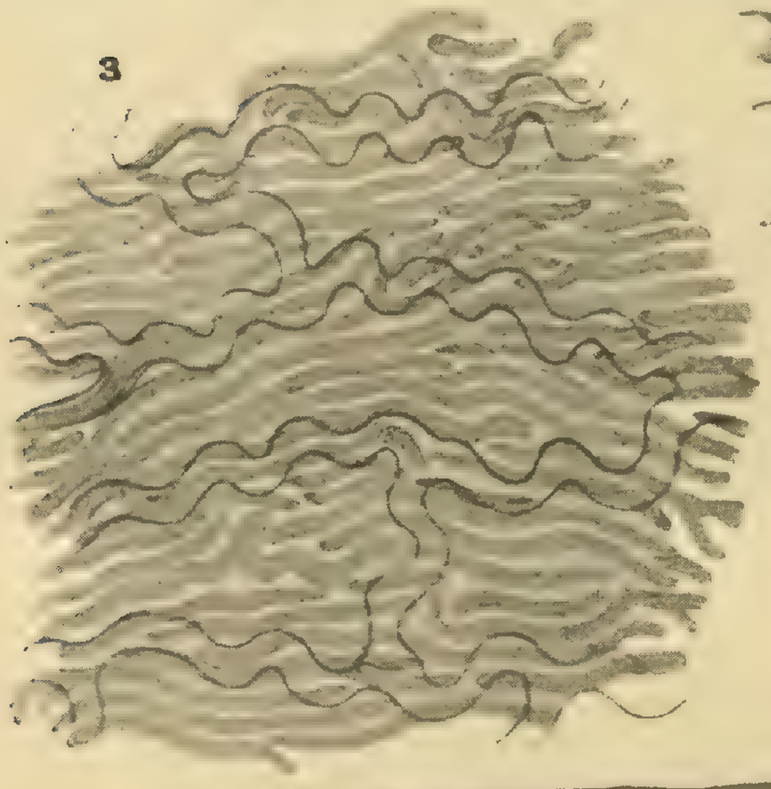
Fig. 12. *Ptilozamites Leckenbyi.* Part of lower epidermis, showing straight-walled cells and stomata. From Gristhorpe. × 200.

Fig. 13. *Ctenis falcata.* Part of lower epidermis with stomata. From Gristhorpe. × 200.



1

2

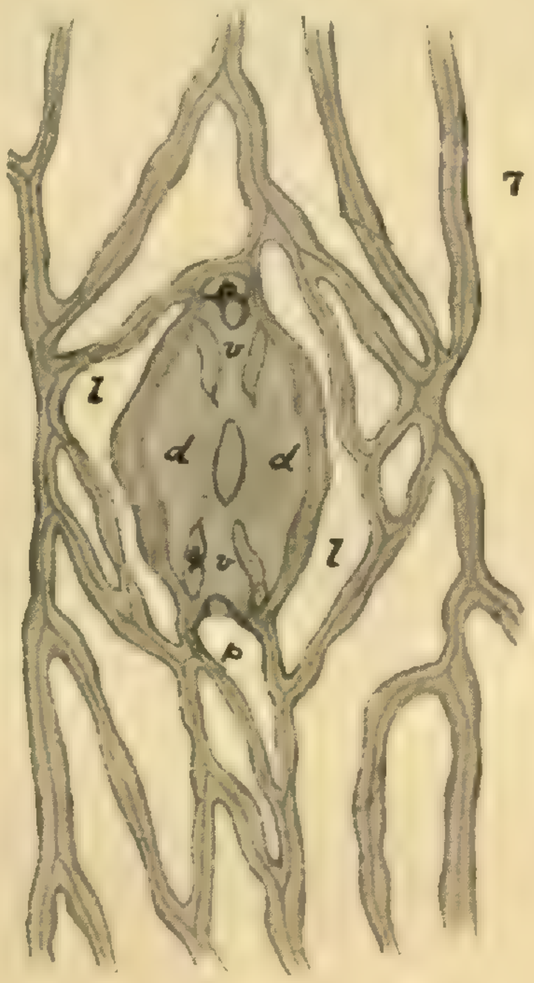


3

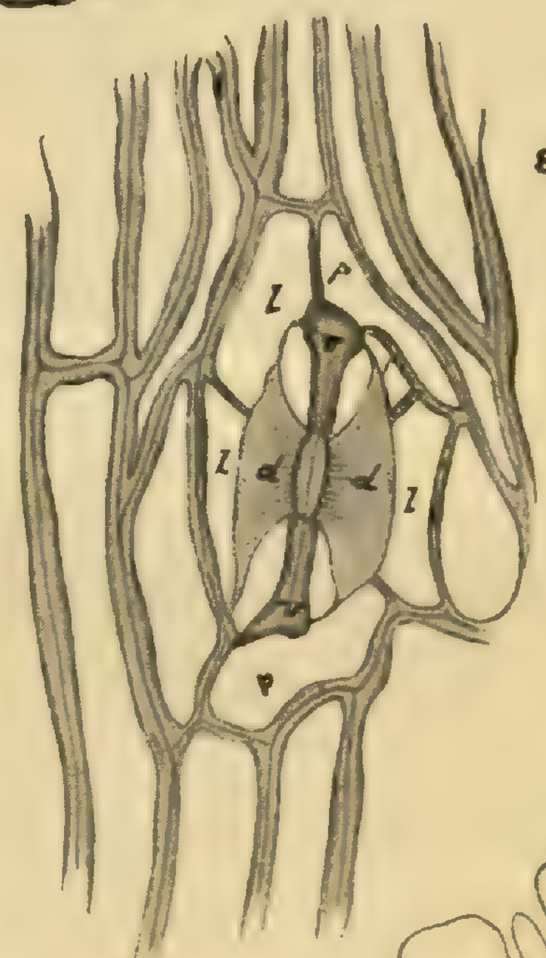
4

5

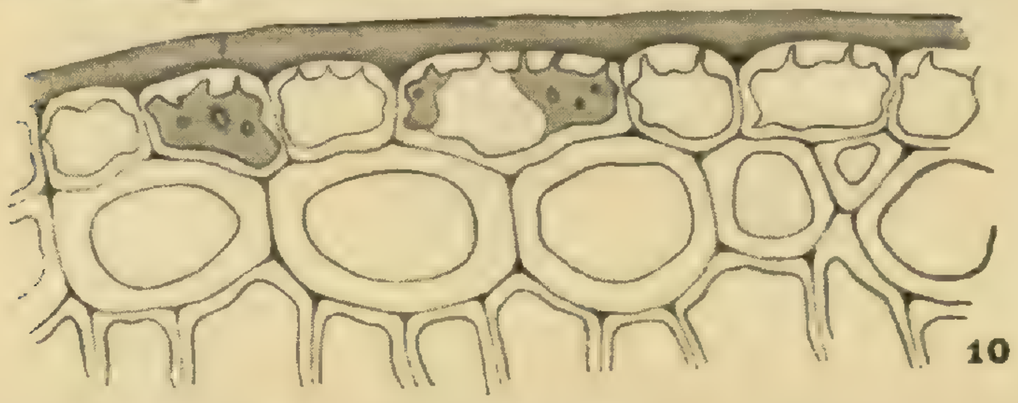
6



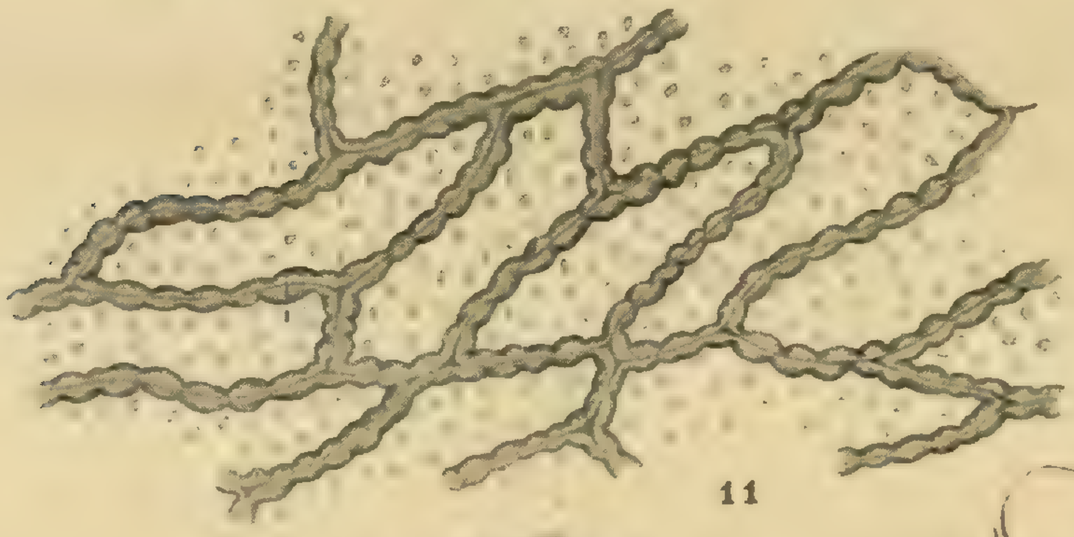
7



8



10



11

12

9

14

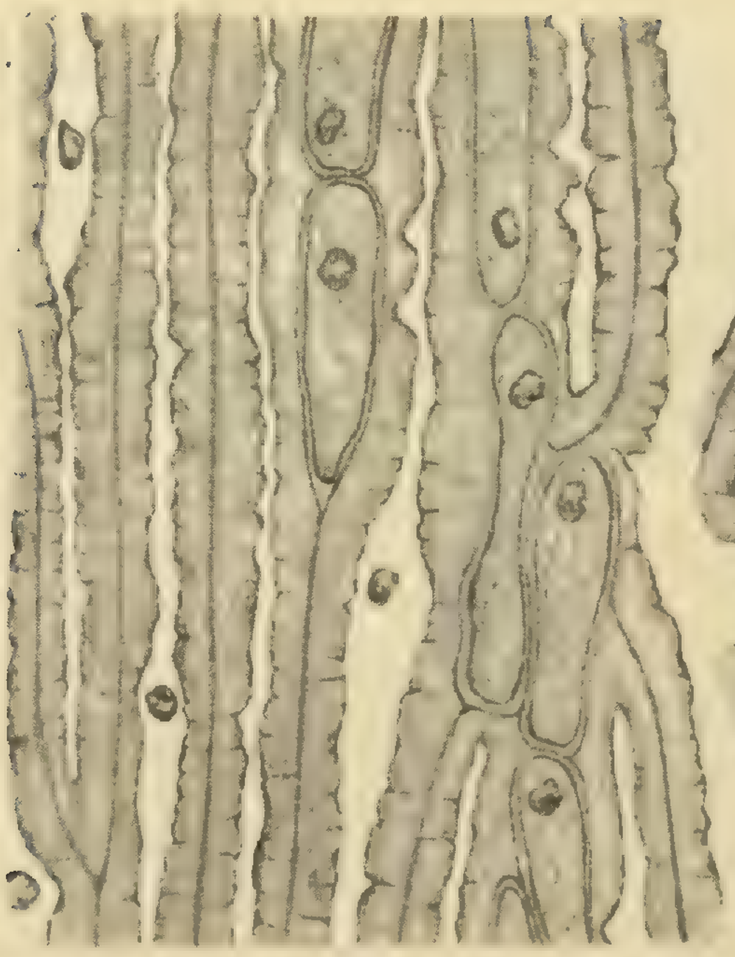
13

15

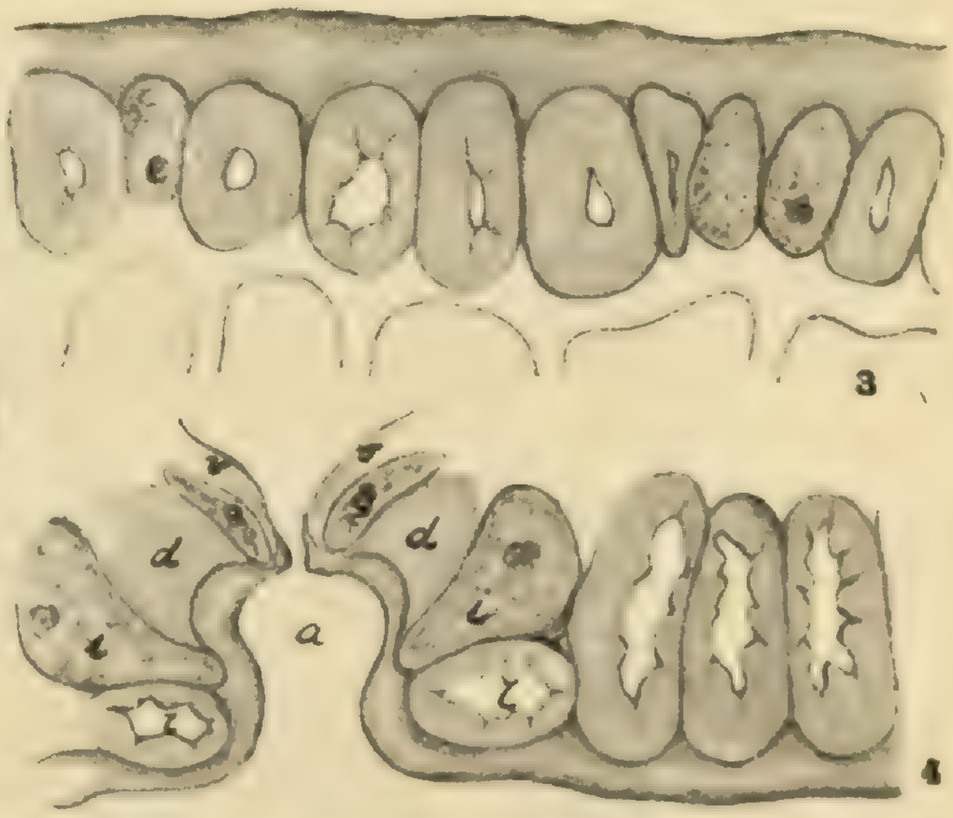
N. B. del.

Grout, sc.

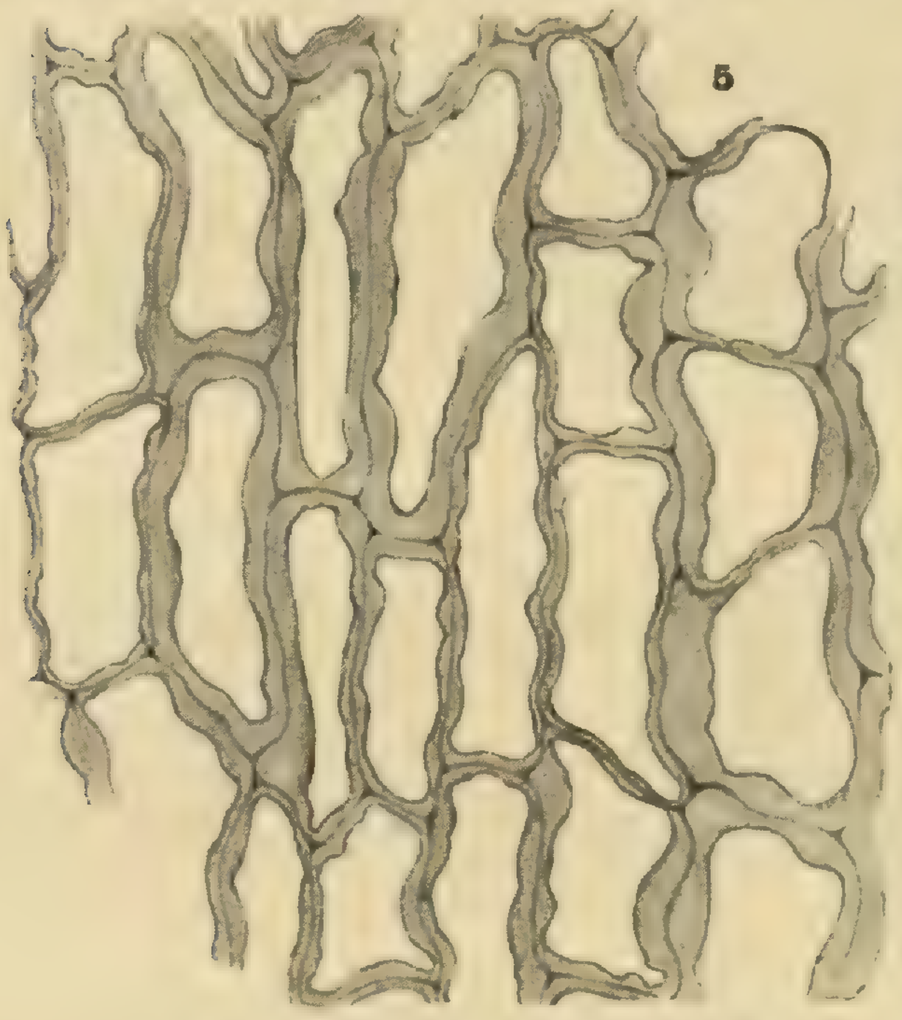
CYCADEAN CUTICLES.


1

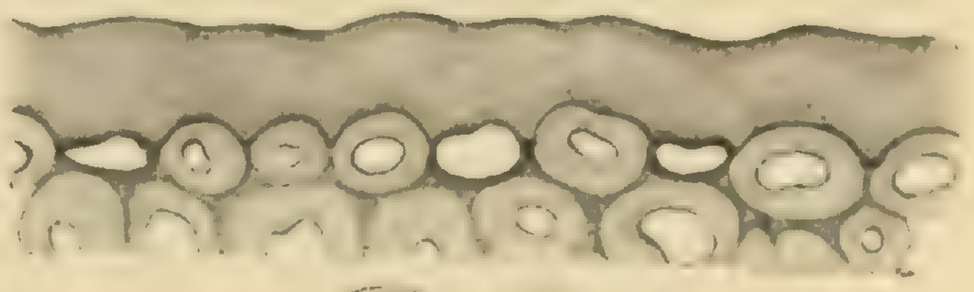
2


3

4

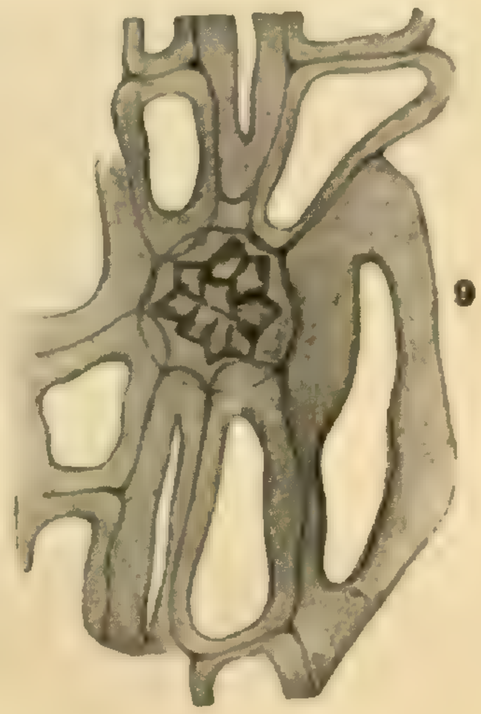

5

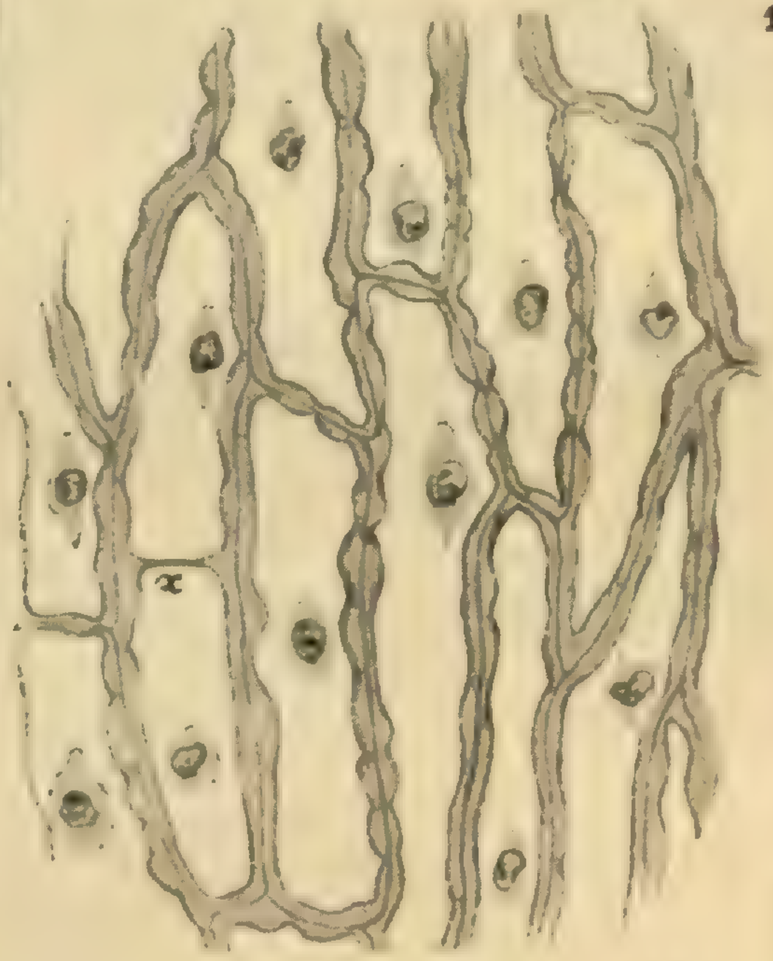
6


7

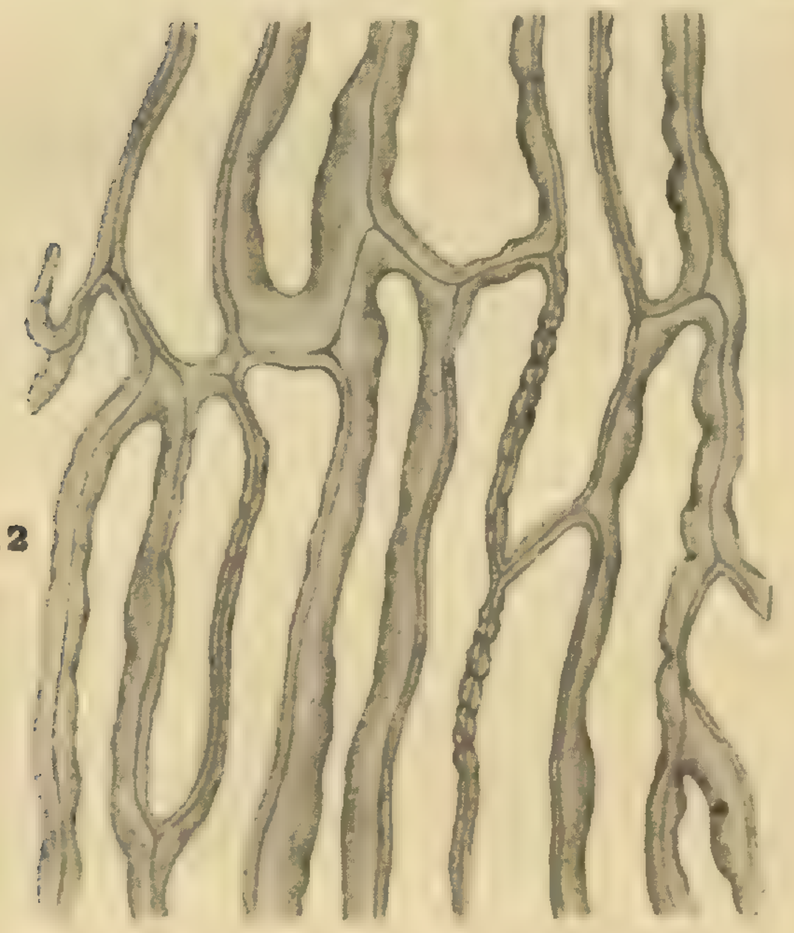
8

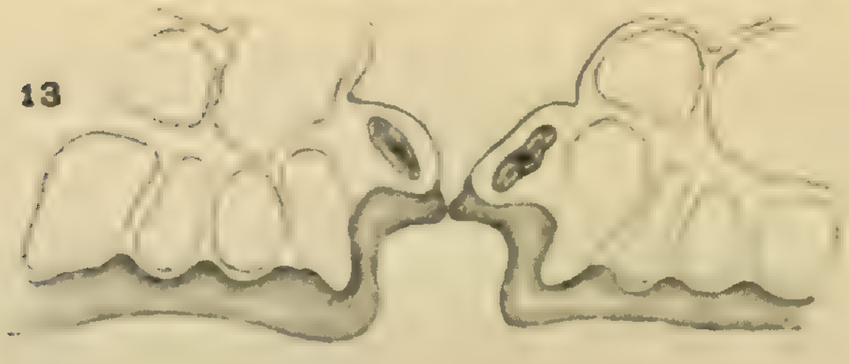
10

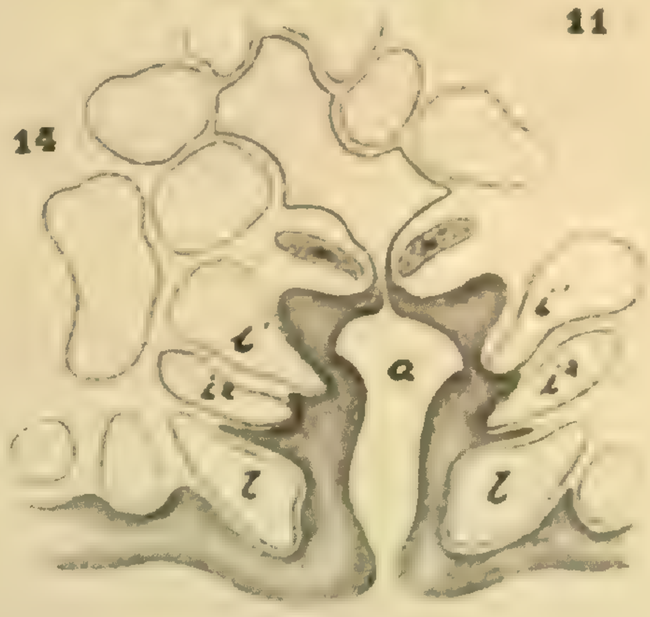

9


11

15


12

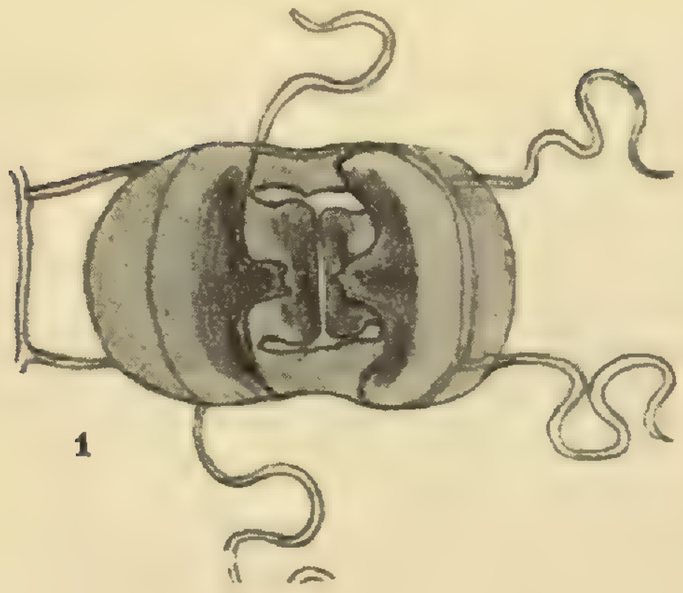

13

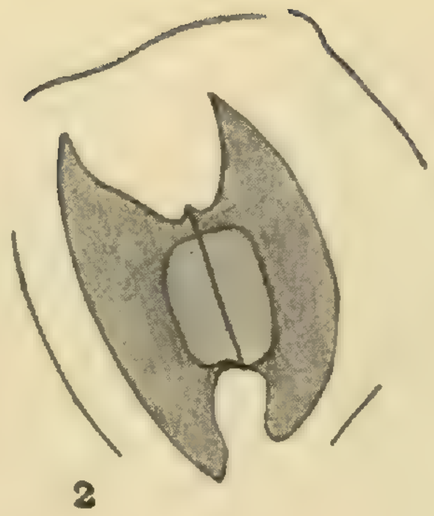


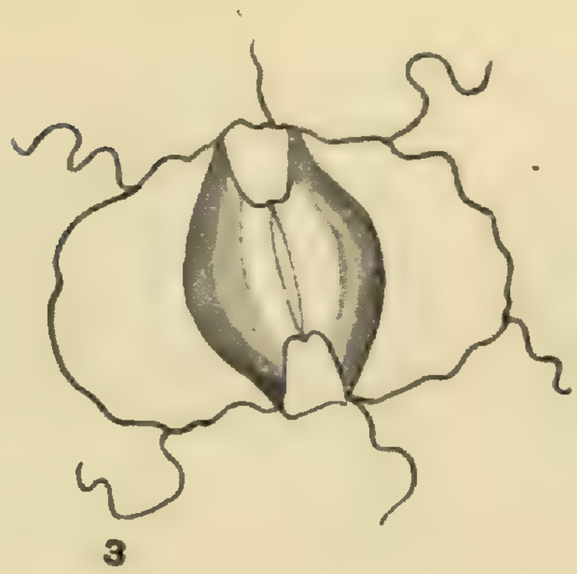
14

N. B. del. Grout, sc.

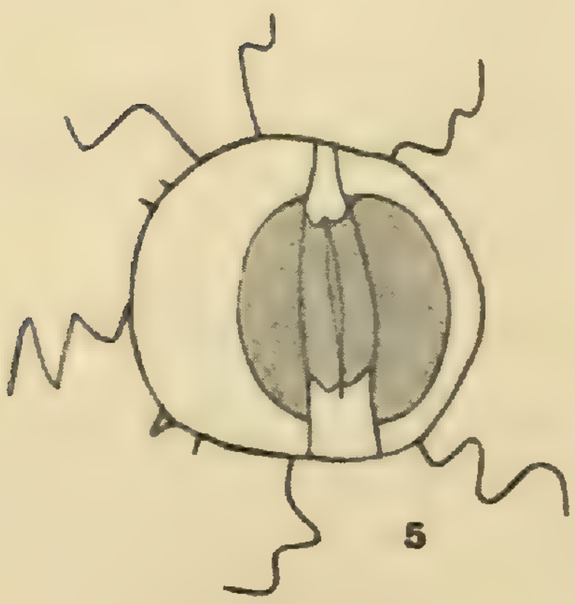
CYCADEAN CUTICLES.

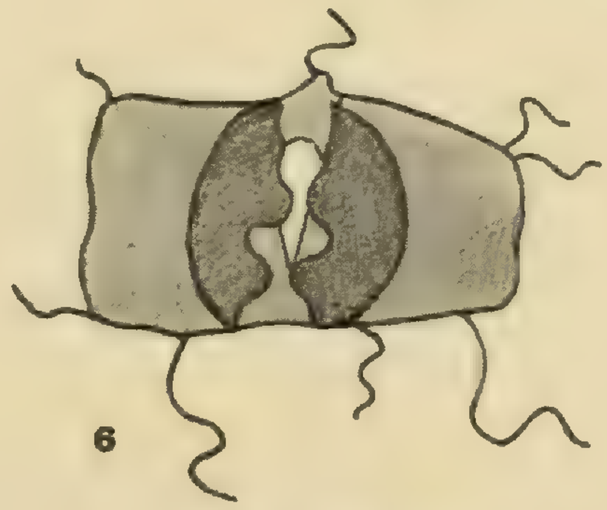

1

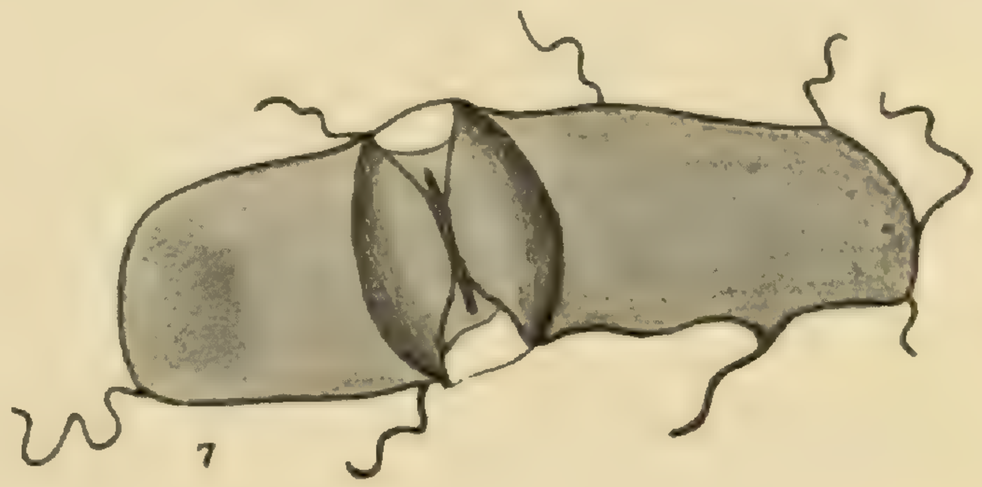

2

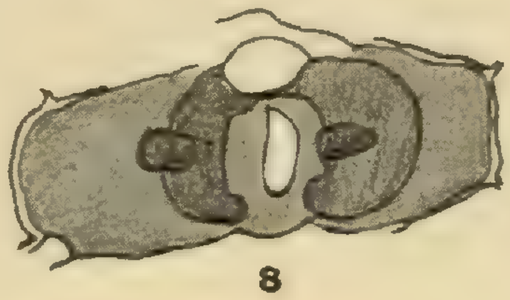

3

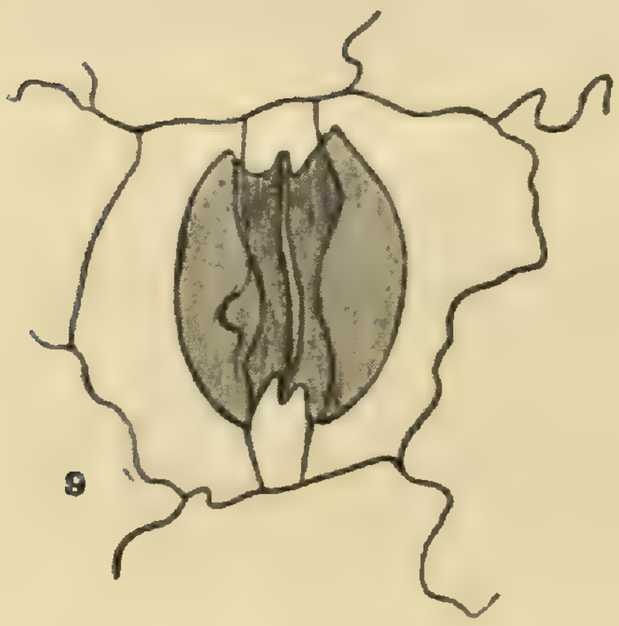
4

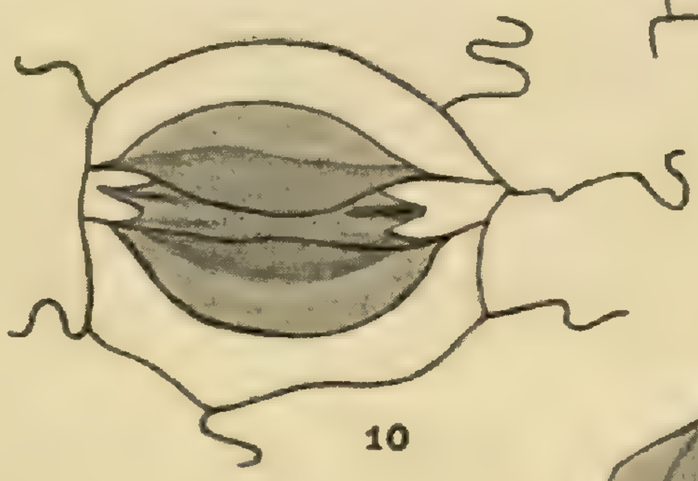

5


6


7

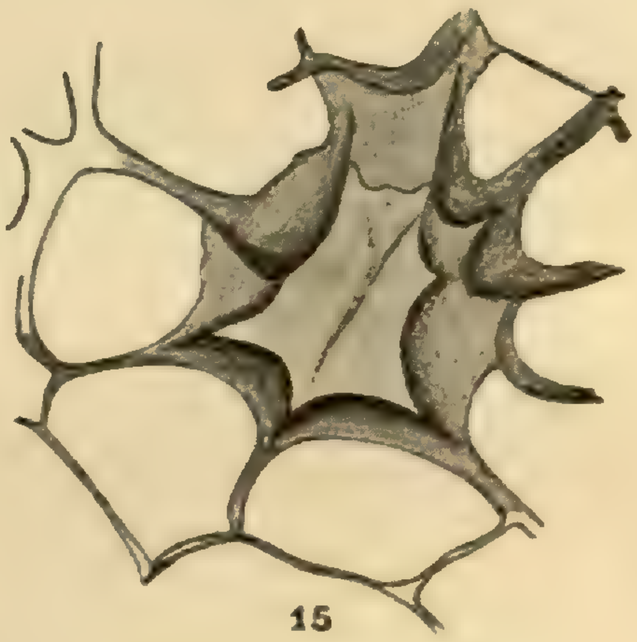

8


9

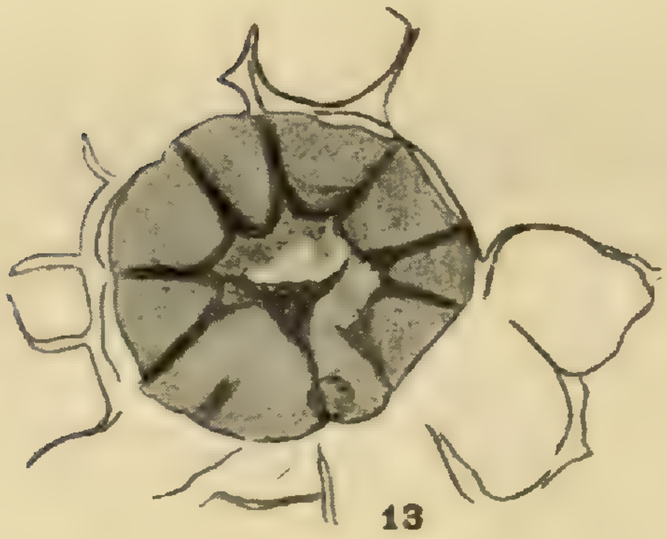

10

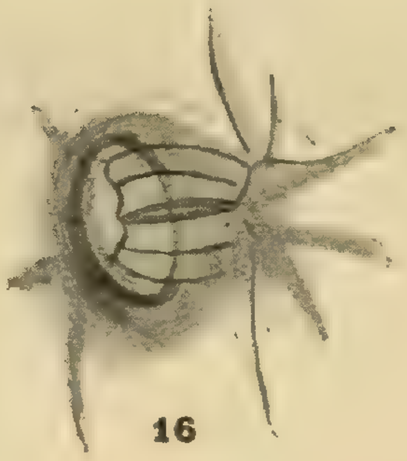
11

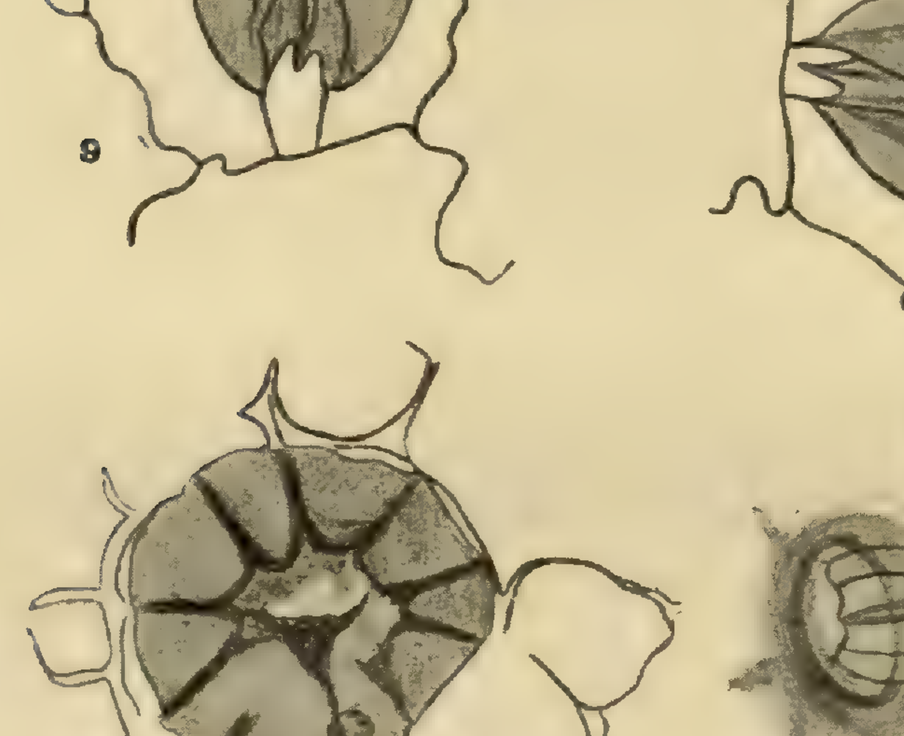
12

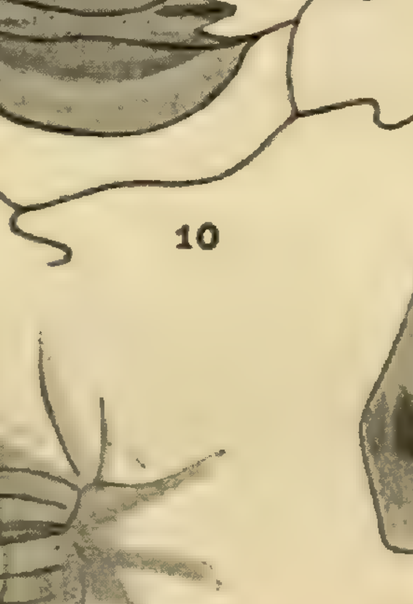

15

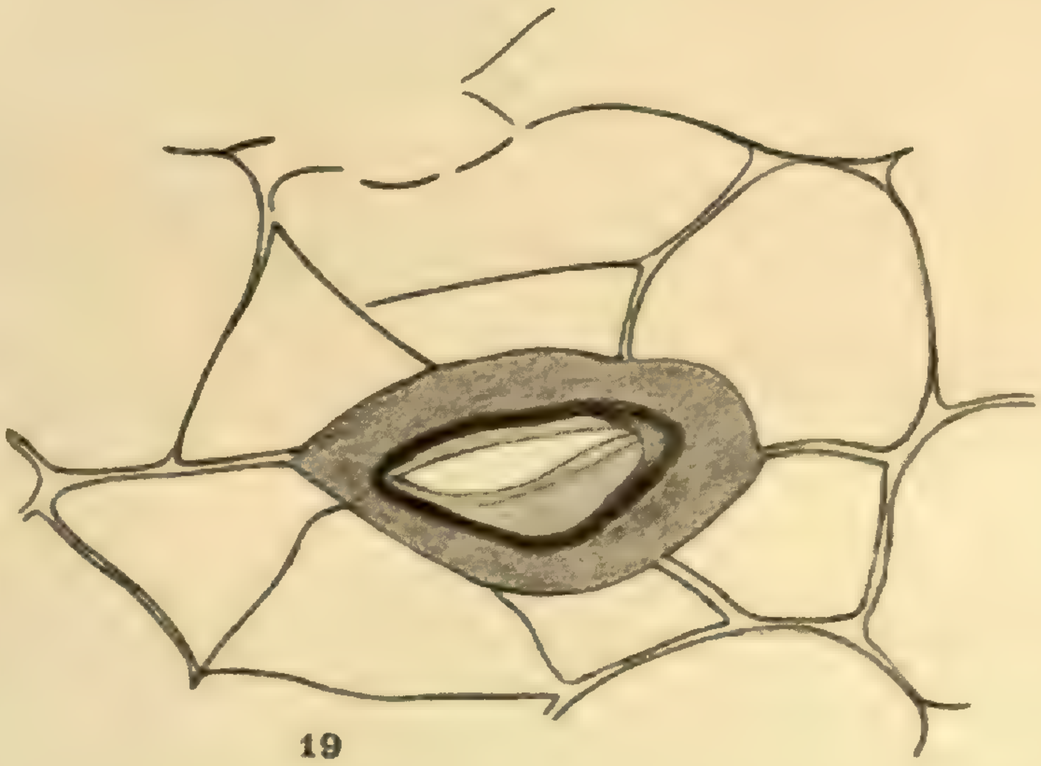
14


13


16


17


18

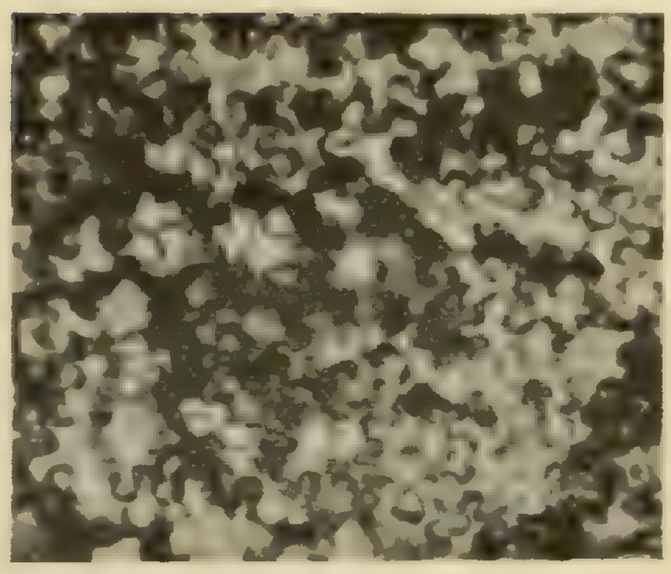

19

H. H. T. del.

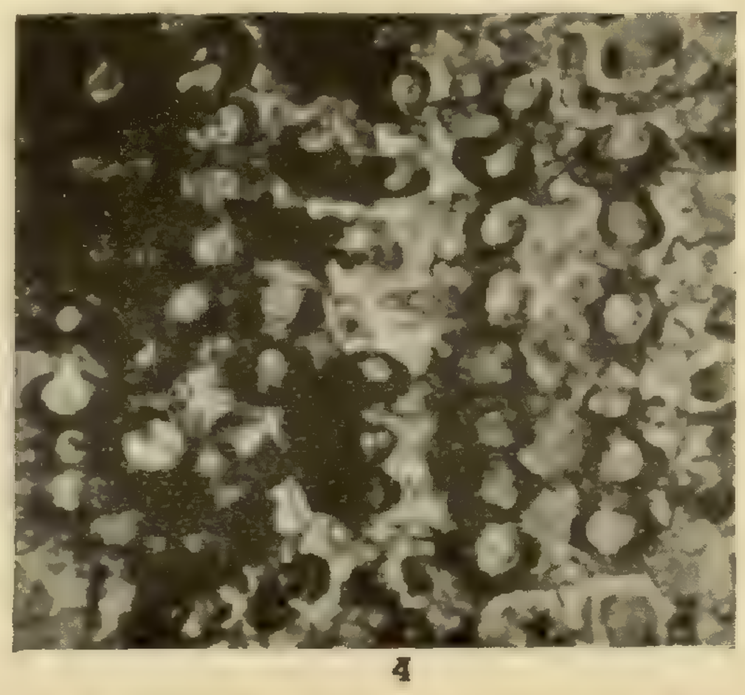
Grout, sc.

CYCADEAN CUTICLES.

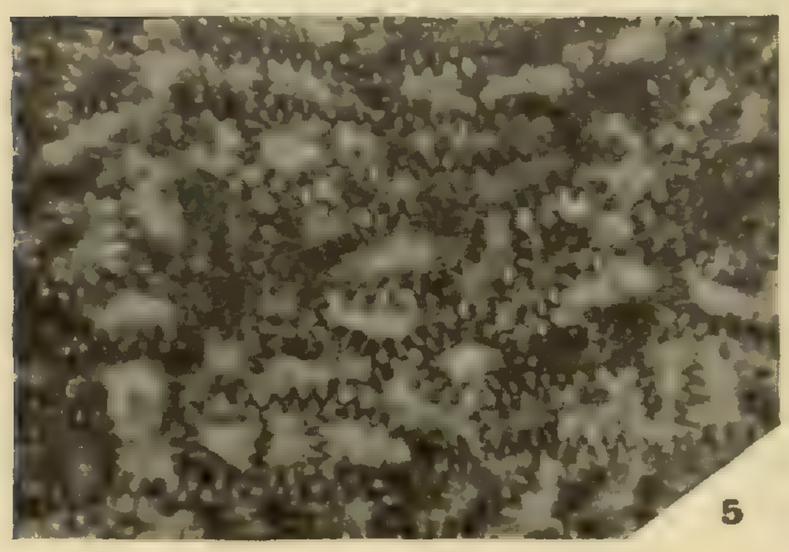
1



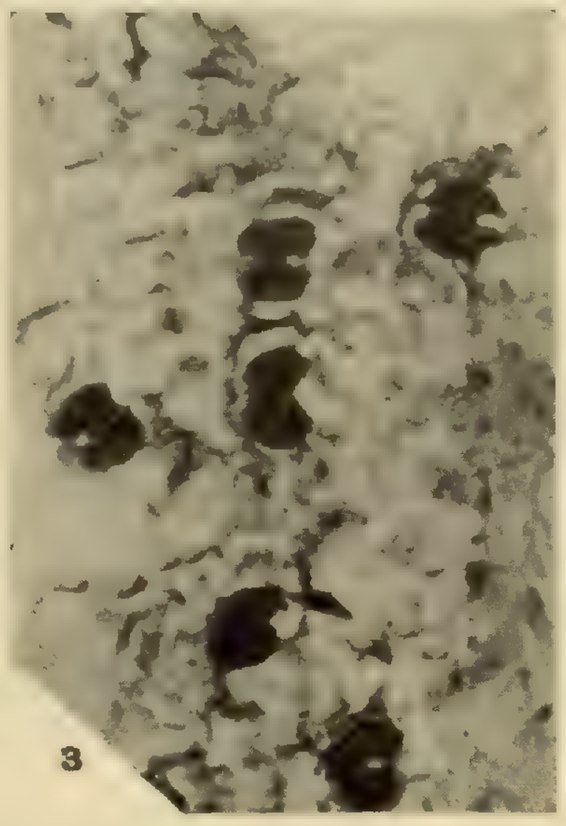
2



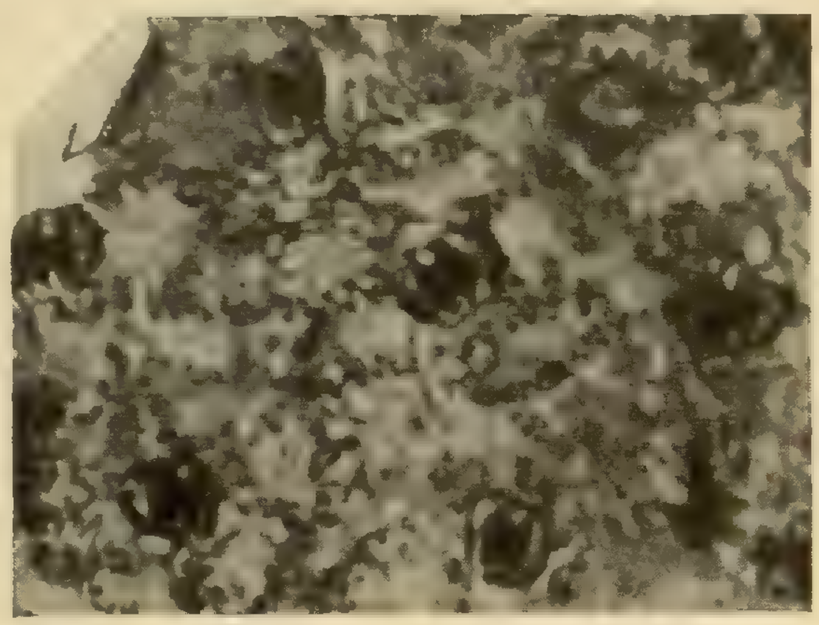
4



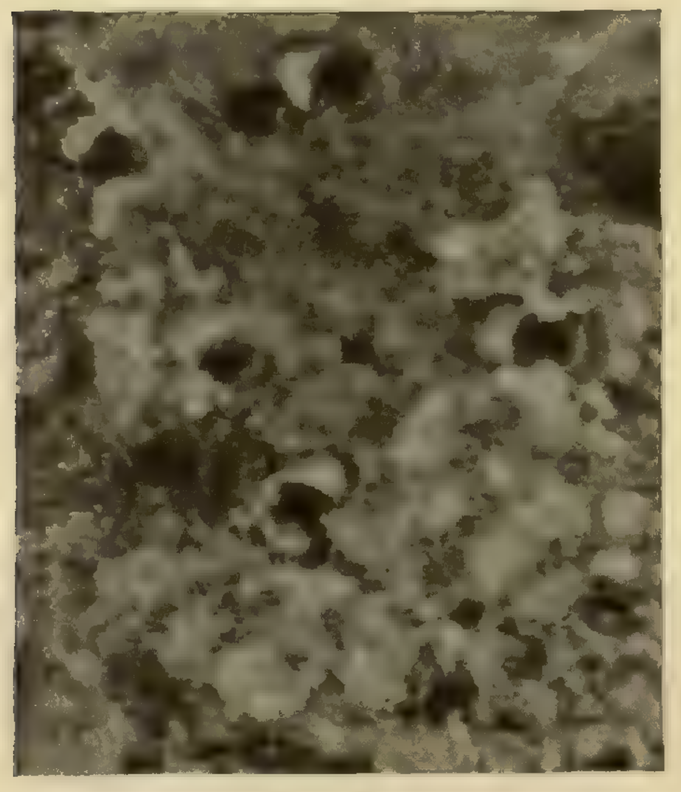
5



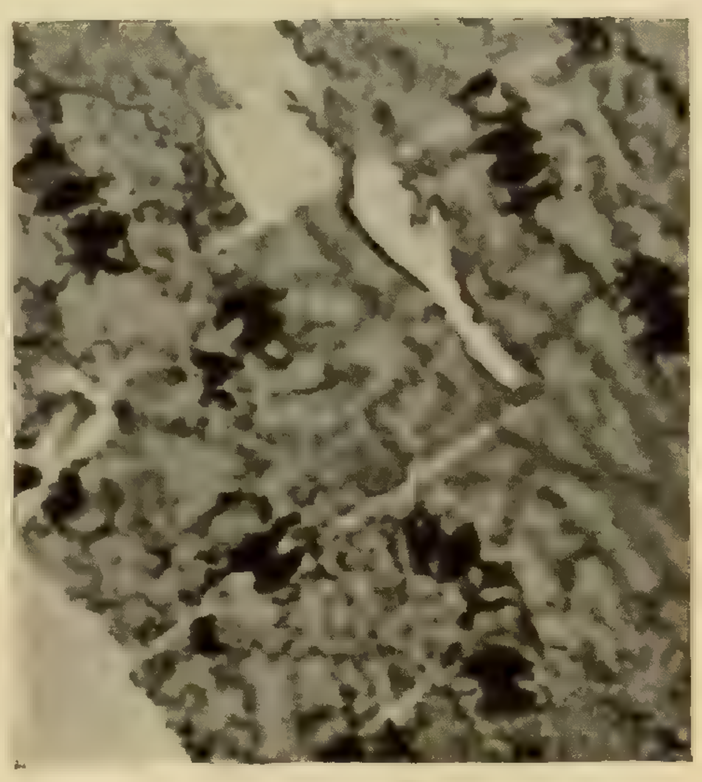
3



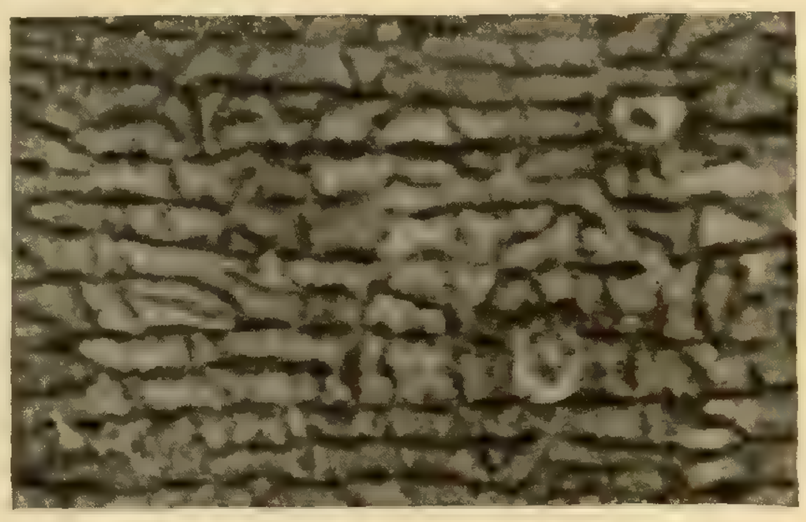
8



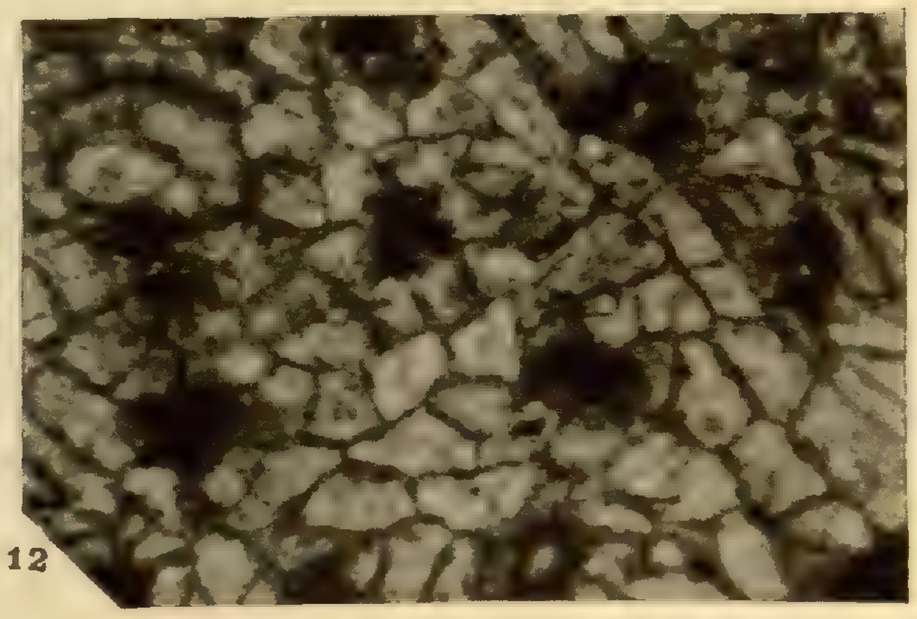
6



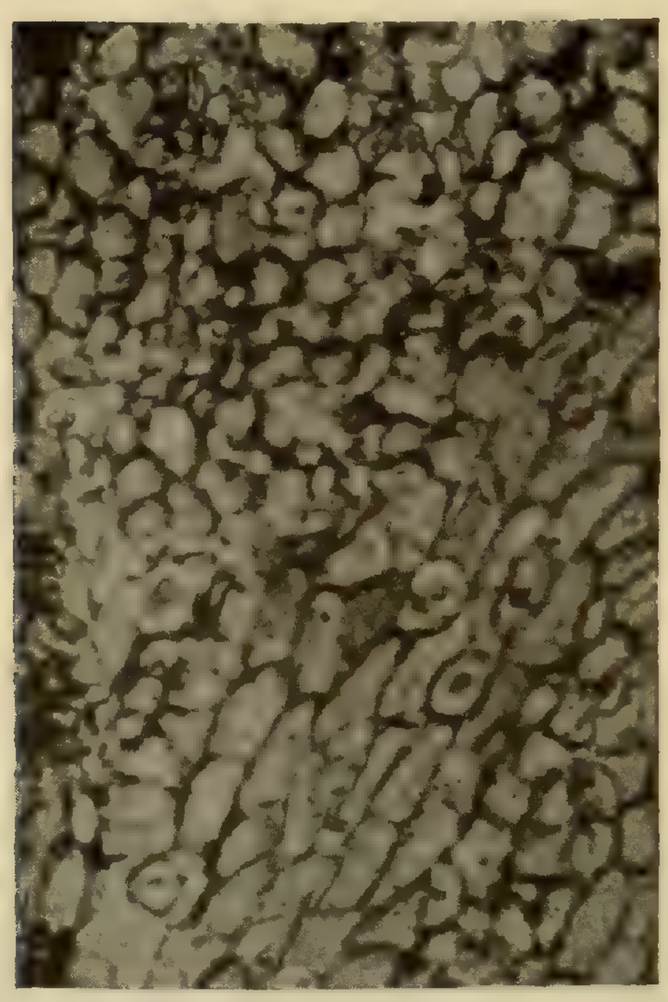
7



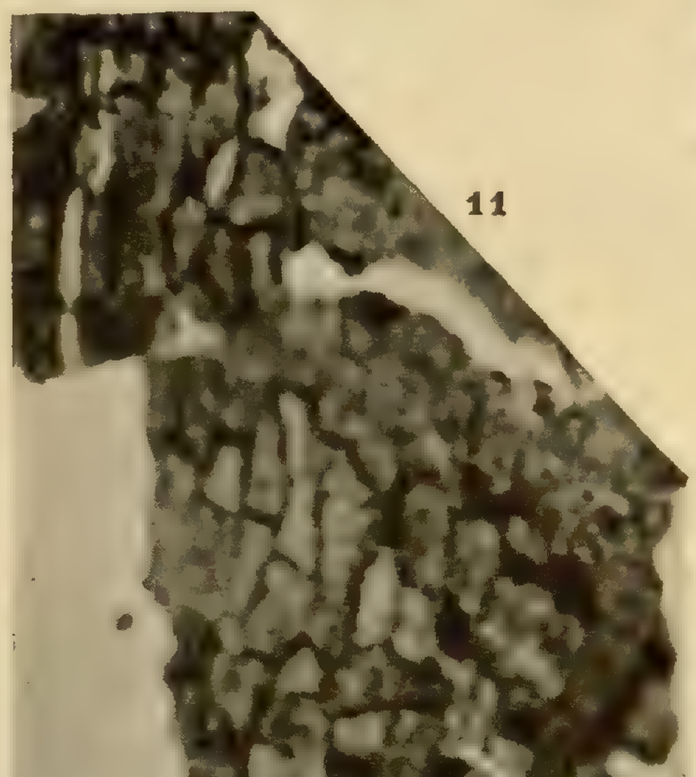
9



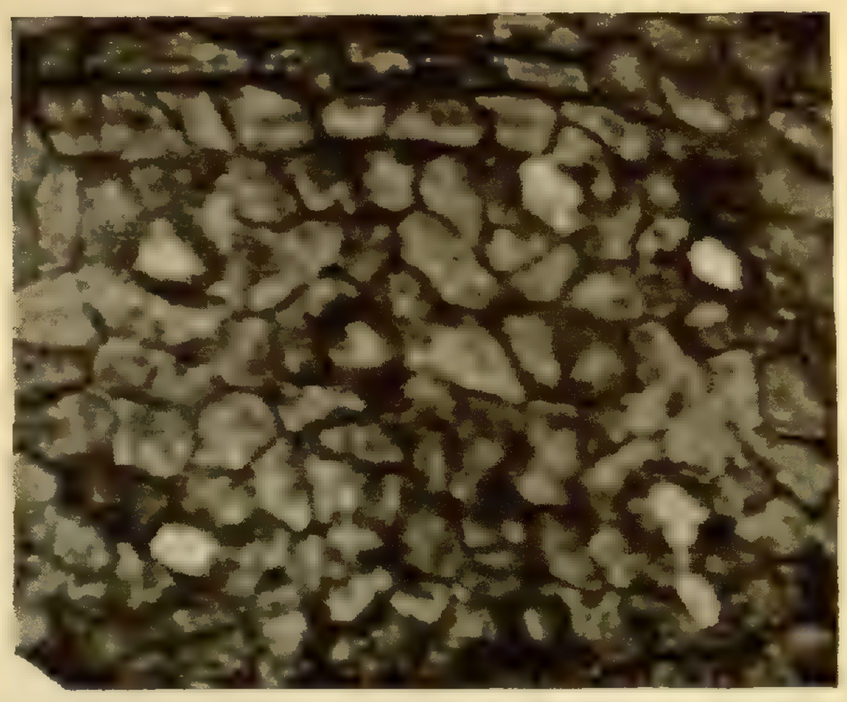
12



10



11



13

H. H. T. phot. Grout, sc.

CYCADEAN CUTICLES.

LINNEAN SOCIETY OF LONDON.

MEMORANDA CONCERNING TRANSACTIONS.

The First Series of the Transactions, containing both Botanical and Zoological memoirs, is now completed in 30 Vols., and a few copies are still for sale. Only complete sets, or parts to complete sets, may be obtained at the original prices. The price of the Index to Vols. I–30 is 2s. to the public, and 1s. to Fellows; to Vols. 28–30, 4s. to the public, and 3s. to Fellows.

The Second Series of the Transactions is divided into Zoological and Botanical sections. The prices of the published parts of these which have been published are as undermentioned. For the Zoological parts see Zoological Supplement.)

Second Series.—Botany.

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
I.	Parts I.–IX. (complete). 1875–80.	3	1	0	0	1	6
II.	Parts I.–XVI. (complete). 1881–88.	6	13	0	5	2	3
III.	Part I. 1888.	3	12	0	2	14	0
	Part II. 1891.	0	5	0	0	3	9
	Part III. 1891.	0	7	0	0	5	3
	Part IV. 1891.	0	6	0	0	4	6
	Part V. 1891.	0	6	0	0	4	6
	Part VI. 1891.	0	3	6	0	2	9
	Part VII. 1892.	0	6	0	0	4	6
	Part VIII. 1893.	0	6	0	0	4	6
	Part IX. 1893.	1	8	0	1	1	0
	Part X. 1894.	0	10	0	0	7	6
	Part XI. 1894.	0	3	4	0	2	6
IV.	Part I. 1894.	1	0	0	0	15	0
	Part II. 1894.	2	0	0	1	10	0
	Part III. 1895.	2	10	0	1	17	0
	Part IV. 1895.	0	3	4	0	2	6
V.	Part I. 1895.	0	9	6	0	6	9
	Part II. 1895.	0	12	0	0	9	0
	Part III. 1896.	0	6	0	0	4	6
	Part IV. 1896.	1	0	0	0	15	0
	Part V. 1896.	0	14	0	0	10	6
	Part VI. 1896.	0	4	0	0	3	0
	Part VII. 1897.	0	4	0	0	3	0
	Part VIII. 1897.	0	6	0	0	4	6
	Part IX. 1899.	0	12	0	0	9	0
	Part X. 1899.	0	6	0	0	4	6
	Part XI. 1899.	0	7	0	0	5	3
	Part XII. 1899.	0	12	0	0	9	0
	Part XIII. 1900.	0	1	6	0	1	2
	Part XIV. 1900.	0	3	0	0	2	3
	Part XV. 1901.	0	6	0	0	4	6

Second Series.—Botany (*continued*).

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
VI.	Part I. 1901.	1	10	0	1	2	6
	Part II. 1901.	0	6	0	0	4	6
	Part III. 1902.	0	18	0	0	13	6
	Part IV. 1903.	0	8	0	0	6	0
	Part V. 1903.	0	8	0	0	6	0
	Part VI. 1903.	0	12	0	0	9	0
	Part VII. 1904.	0	12	0	0	9	0
	Part VIII. 1904.	0	12	0	0	9	0
	Part IX. 1904.	0	7	0	0	5	3
	Part X. 1904.	0	14	0	0	10	6
	Part XI. 1905.	0	4	0	0	3	0
VII.	Part I. 1904.	0	5	0	0	3	9
	Part II. 1905.	0	6	0	0	4	6
	Part III. 1906.	0	3	0	0	2	3
	Part IV. 1906.	0	7	0	0	5	3
	Part V. 1907.	0	10	0	0	7	6
	Part VI. 1907.	0	4	0	0	3	0
	Part VII. 1907.	0	6	0	0	4	6
	Part VIII. 1908.	0	5	0	0	3	9
	Part IX. 1908.	0	2	6	0	2	0
	Part X. 1908.	0	7	0	0	5	3
	Part XI. 1909.	0	4	0	0	3	0
	Part XII. 1909.	0	12	0	0	9	0
	Part XIII. 1909.	0	5	0	0	3	9
	Part XIV. 1909.	0	6	0	0	4	6
	Part XV. 1910.	0	6	0	0	4	6
	Part XVI. 1912.	0	3	0	0	2	3
	Part XVII. 1912.	0	8	0	0	6	0
	Part XVIII. 1912.	0	5	0	0	3	9
	Part XIX. 1912.	0	3	0	0	2	3
	Part XX. Index.	0	3	0	0	2	3
VIII.	Part I. 1913.	1	0	0	0	15	0
	Part II. 1913.	0	8	0	0	6	0
	Part III. 1913.	0	8	0	0	6	0
	Part IV. 1913.	0	4	0	0	3	0
	Part V. 1913.	0	10	0	0	7	6

2nd Ser. BOTANY.] [VOL. VIII. PART 6.

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

AN ANATOMICAL STUDY OF THE PALÆOZOIC CONE-GENUS LEPIDOSTROBUS.

BY

AGNES ARBER, D.Sc., F.L.S.,

FELLOW OF NEWNHAM COLLEGE, CAMBRIDGE.

LONDON:

PRINTED FOR THE LINNEAN SOCIETY

BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON-HOUSE, PICCADILLY, W.,

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

July 1914.

132

VII. *An Anatomical Study of the Palæozoic Cone-genus* Lepidostrobus.

By Agnes Arber, *D.Sc., F.L.S., Fellow of Newnham College, Cambridge.*

(Plates 21–27, and 4 Figures in the Text.)

Read 19th June, 1913.

Contents.

	Page
1. Introduction	205
2. A Survey of our Present Knowledge of the Structure of *Lepidostrobus*	206
3. On certain hitherto Unrecorded Features in the Structure of *Lepidostrobus oldhamius*, Will., and *L. foliaceus*, Maslen	208
4. A Description of some New Forms of *Lepidostrobus*	212
(i.) *L. Binneyanus*, sp. nov.	212
(ii.) *L. gracilis*, sp. nov.	217
(iii.) *L. oldhamius*, Will., f. *minor*	220
(iv.) *L. oldhamius*, Will., f. *pilosus*	223
5. On a Case of Variation in the Anatomical Characters of Different Regions in a Single Cone	228
6. On the Relation between Structure and Function in the Cone-genus *Lepidostrobus*	230
7. List of Memoirs cited	232
8. Explanation of the Plates	233

1. Introduction.

The collection of fossil plants in the Sedgwick Museum, Cambridge, includes sections of certain specimens of *Lepidostrobus*, which differ considerably from those members of this cone-genus whose structure has been previously described. The present memoir is based upon a study of these sections, and also of a large number of preparations from other collections. In this connection I would express my great indebtedness to those botanists who have kindly lent me sections of these cones and allowed me to describe them,—Dr. W. J. Jongmans, Professor F. W. Oliver, F.R.S., Dr. D. H. Scott, F.R.S., Miss Winifred Smith, Mr. D. M. S. Watson, and Professor Weiss. To Dr. Scott, I must, in addition, offer my thanks for the help and information he has kindly given me. I have also to thank Dr. A. Smith Woodward, F.R.S., the Keeper of the Department of Geology, British Museum (Natural History), for allowing me opportunities of studying the specimens under his charge. Certain sections, which have been of use in this investigation, have been purchased by aid of a grant from the British Association, for which I am much indebted.

Finally, I wish to express my gratitude to Professor T. McKenny Hughes, F.R.S., who has given me every facility for carrying out this work in the Sedgwick Museum.

2. A Survey of our Present Knowledge of the Structure of *Lepidostrobus*.

The general characters of the cone-genus *Lepidostrobus* are too familiar to need recapitulation here. In all essentials this genus is a remarkably uniform one. We are fortunate in having a fairly complete knowledge of several species which have been found in the petrified state, and it may be useful, before dealing with the observations contained in the later sections of the present paper, to refer very briefly to these cones and their structure.

One of the first *Lepidostrobi* of which the internal structure became known, was *L. Brownii*, (Unger) Schpr., a large cone from the Lower Carboniferous rocks, which was originally described by Robert Brown *. We have recently been put into possession of detailed knowledge of this species, and of one or two other cones closely related to it, by means of Zeiller's † exhaustive and beautifully illustrated monograph. The strobilus has several peculiar features, the most striking of which are the following: the lamina of the sporophyll terminates in a swollen cushion, and trabeculæ of sterile tissue arise from the floor of the sporangium and penetrate among the spores. No megaspores have been discovered.

Another Lower Carboniferous cone whose structure is preserved is *Lepidostrobus Veltheimianus*, Scott, a heterosporous form from the Calciferous Sandstone of Burntisland, first described by Williamson ‡. This is a small and slender cone, similar in general structure to the familiar *L. oldhamius* of the Coal Measures. A delicate radial plate of sterile tissue arises from the floor of the microsporangium, and penetrates some distance into the sporangial cavity.

From the Calciferous Sandstone we have also another heterosporous cone, *Lepidostrobus Wünschianus*. The structure of this strobilus was described and figured by Binney §, not, however, in microscopic detail.

The best known *Lepidostrobus*, which occurs as a petrifaction in the Upper Carboniferous rocks, is the Coal Measure form *L. oldhamius*, originally described by Williamson ‖. Binney ¶, at an earlier date, had described and figured, under the name of *Lepidodendron Harcourtii*, sections from the identical specimen upon which Williamson afterwards based the species *oldhamius*. Binney also described other sections of the same type of cone, attributing them to *L. vasculare*. More recently Maslen ** has redescribed *Lepidostrobus oldhamius* in detail, with special reference to Williamson's slides. The cone of this species is larger than that of *L. Veltheimianus*, but smaller than that of *L. Brownii*. No megasporangia have been up till now

* Brown, R. ('48) and ('51). For another early account of some members of the genus see Hooker, J. D. ('48).
† Zeiller, R. ('11). ‡ Williamson, W. C. ('73), p. 294 and pl. 44. § Binney, E. W. ('71), pl. 11.
‖ Williamson, W. C. ('94), pp. 27 & 28, pl. 9. fig. 58, pl. 6. figs. 61 & 62.
¶ Binney, E. W. ('71), p. 46 etc., and pls. 7 & 8. ** Maslen, A. J. ('99).

described. The sporophyll has a thin, leafy lamina, quite different from the cushion-like body which terminates the sporophyll lobe of *L. Brownii*. The distal end of the sporangium is peculiar in arching over and concealing the ligule. The latter organ, which was first discovered by Maslen * in this species, now appears to be present universally in connexion with the sporophylls of *Lepidostrobus*. Maslen † distinguishes within the species *L. oldhamius* three forms, which he calls (α), (β), and (γ). The chief differences between these types lie in the anatomical structure of the axis. Maslen's form (β) represents the species as originally described by Williamson.

Coulter and Land ‡ have described a petrified cone from the Coal Measures of Iowa which appears to belong to the type of *L. oldhamius*.

The structure of a large cone from the Upper Carboniferous (Westphalian) of the Donetz basin has recently been discussed in great detail by Zalessky §, who has named it *Lepidostrobus Bertrandi*. This fructification does not differ in any essential anatomical feature from *L. oldhamius*, but, at the same time, there is no doubt that it represents a distinct species.

Homosporous or microsporous cones of the type of *L. oldhamius* are not, however, the only forms of *Lepidostrobus* met with in the Upper Carboniferous rocks. Williamson ‖ gives a figure of a section of a slender cone from the Coal Measures which differs markedly from both *L. oldhamius* and *L. Bertrandi*. In Williamson's text this section is dismissed with a brief mention, and we had no detailed information about it until it was redescribed by Maslen ¶ under the name of *L. foliaceus*. The form of the sporophyll and the histology of the lamina are peculiar, and make it easy to recognise the species at a glance. Williamson's section contained only microspores, but our knowledge of the cone has now been rendered much more complete by Mrs. Scott's ** discovery that certain megaspores with peculiar appendages, with which she had been acquainted for some time as isolated objects, were borne in sporangia which belonged to *L. foliaceus*. This species thus ranks as a heterosporous *Lepidostrobus*.

Little is known with certainty on the subject of the attribution of these various cones to the species of *Lepidodendron* which bore them. Williamson †† pointed out that it was extremely probable that the heterosporous cone, which he described from Burntisland, was the fructification of *Lepidodendron Veltheimianum*, and Scott ‡‡ has confirmed this attribution and employed the name *Lepidostrobus Veltheimianus* for the cones. In *Lepidostrobus Wünschianus*, another heterosporous cone from the same horizon found in Arran, we appear to have a second instance in which the structure both of the stem and the strobilus are known §§. These two species seem, however, to be the only instances in which we are definitely acquainted with the internal structure both of the fructification and of the tree which bore it.

In certain cases it is possible to identify cones whose internal structure is preserved

* Maslen, A. J. ('98). † Maslen, A. J. ('99). ‡ Coulter, J. M., & Land, W. J. G. ('11).
§ Zalessky, M. ('08). ‖ Williamson, W. C. ('94), p. 27, and pl. 9. fig. 57.
¶ Maslen, A. J. ('99), p. 373, and pl. 38. figs. 36–39. ** Scott, R. ('06).
†† Williamson, W. C. ('73), p. 94. ‡‡ Scott, D. H. ('00), p. 171.
§§ Binney, E. W. ('71), p. 56, pl. 11, and Williamson ('94), p. 29.

with others which we know only as impressions. It is probable, for instance, that *Lepidostrobus oldhamius* may be identical with the cone-impressions known as *L. variabilis*, Lindl. & Hutt., which are so common in the Coal Measures. Generally, however, it is extremely difficult to correlate "impressions" and "petrifactions" of cones. Several reasons for this difficulty readily suggest themselves. The features, about which we obtain most information from petrified material, are the anatomy of the axis and of the sporophylls, and the internal structure of the sporangium. The general shape and dimensions of such cones are often imperfectly known, and the external form of the sporophylls and sporangia is frequently difficult to reconstruct. In "impressions" of cones, on the other hand, it is just these external features about which information is easiest to obtain, while such material gives little clue to those characters which we know in the greatest detail from petrified fructifications.

Another cause of difficulty in correlation appears to be that the cones of these species, which lend themselves most readily to entire or partial survival as impressions, are often ill-adapted to preservation as petrifactions. We occasionally find, in the Coal Measures, impressions of extremely large, detached sporophylls of *Lepidostrobus*. There is, for example, a specimen in the Sedgwick Museum * in which the lamina reaches the length of 8·9 cms. It seems obvious that a cone protected by the overlapping lobes of such sporophylls would prove highly resistant to the infiltration of any petrifying material. This may perhaps explain why it is that none of the cones with well-preserved internal structure which have been described from the Coal Measures, possess sporophylls approaching these dimensions.

In a later section of this paper some account is given of certain forms of *Lepidostrobus* which do not appear to have been hitherto described. In none of these cases is it at present possible to correlate the petrified cone with the stem which bore it, or with impressions showing surface features.

3. On certain hitherto Unrecorded Features in the Structure of *Lepidostrobus oldhamius*, Will., and *L. foliaceus*, Maslen.

(i.) *The Existence of a Sterile Plate in the Sporangium of* L. oldhamius *and* L. foliaceus.

The type sections of Williamson's species, *L. oldhamius*, consist, as Maslen † has pointed out, of two slides now in the Williamson Collection, British Museum (C.N. 568 & 574); in addition there are certain slides in the Binney Collection, Sedgwick Museum, Cambridge, which were cut from the same cone. Sections of another cone in the Williamson Collection, known as "Wild's Cone" (C.N. 1776 A & B), are also attributed by Maslen to the type form. The preparations of the latter cone are

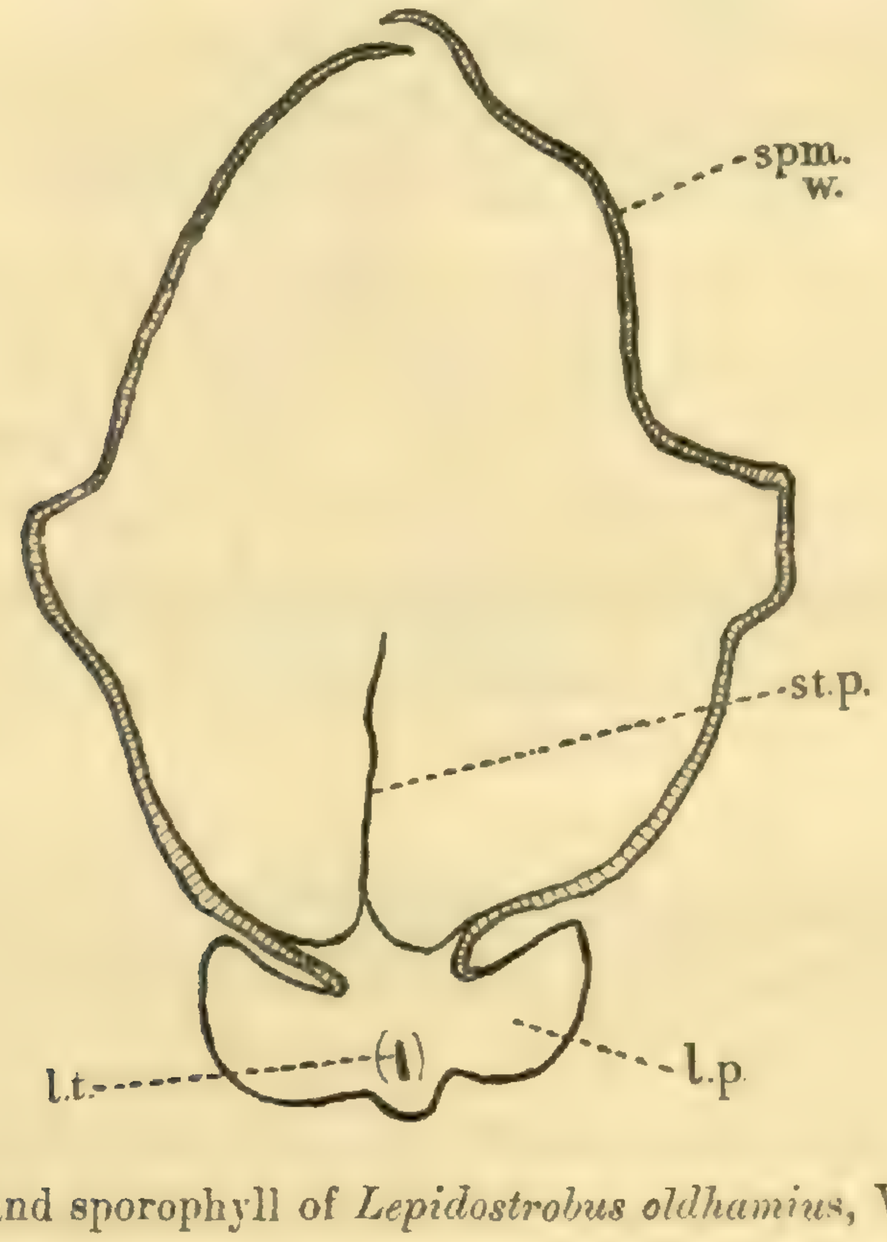
* *Lepidophyllum majus*, Brongn. From the Upper Coal Measures, Coal Pit Heath Colliery, near Bristol. Sedgwick Museum Coll., 2076.

† Maslen, A. J. ('99), p. 359.

particularly valuable, on account of the good preservation of the structures external to the axis.

When examining Wild's Cone, I was struck by a feature which has not been recorded as occurring in this species—the presence, namely, of a delicate radial plate of sterile tissue arising from the floor of the sporangium and appearing in tangential sections merely as a streak * (Text-fig. 1). It resembles the outgrowth figured by Williamson † in

Text-fig. 1.



Radial section of a sporangium and sporophyll of *Lepidostrobus oldhamius*, Will., "Wild's Cone," *Williamson Collection*, Brit. Mus. (Nat. Hist.) C.N. 1776 B. (× 32 circa.)

(*l.p.* = sporophyll pedicel; *l.t.* = sporophyll trace; *spm.w.* = sporangium wall; *st.p.* = plate of sterile tissue arising from the floor of the sporangium.)

the case of *L. Veltheimianus*, except that it does not, as a rule, bifurcate, although it may occasionally branch at the apex. It happens that, in the case of Williamson and Binney's original cone, there are scarcely any good tangential sections passing through a sporangium attached to its sporophyll; so we cannot get a view of the sterile plate comparable with that obtained in the preparation of Wild's Cone. In one of the sections of the original cone in the Binney Collection ‡, however, two of the sporangia are cut with great exactness in the radial plane, and in both these cases there are distinct indications of the presence of a plate of sterile tissue arising from the floor of the sporangium and lying approximately in the plane of section.

That this plate of sterile tissue within the sporangium is actually characteristic of the type form of *L. oldhamius* is confirmed by certain sections in Dr. Scott's Collection. A sporophyll with a sporangium from one of these § is shown in Pl. 27. fig. 55.

* Other sections of Wild's Cone are preserved in the Manchester University Collection, and here the sterile plates can also be observed; *e. g.*, R. 384 *b*.

† Williamson, W. C. ('73), p. 295 & pl. 44. figs. 23, 24, 25.

‡ Binney Coll., No. 87.

§ Scott Coll., 2456.

In this case the sterile upgrowth (*st. p.*) is usually well preserved and can be seen to consist of delicate cellular tissue. The sterile plate is still better displayed in certain sections of sporangia near the apex of a cone of *L. oldhamius* which occur in a preparation in the University College Collection * (Pl. 24. fig. 17). The most remarkable instances of sterile plates with which I am acquainted, however, are to be found in a series of obliquely transverse sections of a cone from Shore, Littleborough, preserved in the Leiden Herbarium (Slides 211–214). A single section, which obviously, from internal evidence, belongs to the same series and must have been cut from this identical cone, has been presented by Miss Winifred Smith to the Sedgwick Museum, Cambridge †. From a study of the latter section alone, I originally drew the conclusion that this cone represented a new species, to which, in a preliminary note ‡, I gave the name *Lepidostrobus laminatus*. An examination of the Leiden slides, which I have recently had the opportunity of making, through the kindness of Dr. Jongmans, has convinced me that the cone in question is not specifically different from *L. oldhamius*; the name *L. laminatus* must hence be discarded. The sections of the cone are useful because they pass obliquely through the apex and display the internal structure of immature sporangia with great clearness. The sterile plates in these young spore-sacs are massive and well preserved, and give rise with great regularity to two smaller lateral processes, one on either side (*st.p.*, Pl. 21. figs. 1 & 3 and Pl. 24. figs. 15 & 16). The branches are not directly opposite to one another, and the main process is continued above its branches for a considerable distance. That these outgrowths are of the nature of plates, running in the direction of the long axis of the sporangium, and are not merely peg-like structures, is evidenced by the fact that they present a general similarity of appearance in the seven sporangia in which they are visible in the section represented in Pl. 21. fig. 1. These sporangia, owing to the fortunate obliquity of the section, are cut at varying distances from the main axis, and we are hence enabled to visualise the structure of a complete individual sporangium. Another point, which is established by the comparison of the different sporangia, is that the sterile plate died out towards the distal end of the spore-sac. The lowest sporangium figured in Pl. 24. fig. 15, which is also shown photographically in Pl. 21. fig. 2, is obviously cut through near the distal end, since the ligule (*lg.*) is visible. In this case there is no sterile upgrowth from the "sub-archesporial pad" §. The structure of one of the sterile processes is shown in detail in Pl. 24. fig. 16. In the older sporangia the sterile plates are relatively less important; the lateral branch-plates seem to shrivel and disappear quite early.

The type section of *Lepidostrobus foliaceus*, Maslen (Williamson Coll., C.N. 1614), is approximately radial, but more or less tangential in the middle region. In at least two sporangia there are indications of a sterile plate similar to that just described in

* U.C.L. Coll., C. 19.

† Slide 281, Sedgwick Museum Coll. This section probably belongs between Slides 213 and 214 of the Leiden Herbarium Coll.

‡ Arber, A. ('13).

§ Bower, F. O. ('94), p. 513.

L. oldhamius. The same feature is also observable in certain sections of the species in the Manchester University Collection *.

The structure which we have been considering is not confined to *L. oldhamius* and *L. foliaceus*, but is found, in addition, in the new forms of *Lepidostrobus* which will be described later in the present paper. It has also been previously recorded in *L. Veltheimianus* † and in an unnamed species ‡ from the Coal Measures; while sterile upgrowths, taking the form of pegs rather than plates, are known in *L. Brownii* §. I am hence inclined to think that the occurrence of some form of sterile upgrowth from the sporangial floor may eventually prove to be characteristic of all forms of *Lepidostrobus* ‖ which are microsporous or homosporous; such a structure does not seem at present to have been recognised in any megasporangium. The fact that these sterile plates have been hitherto overlooked in so well-known a type as *L. oldhamius* is no doubt due to the circumstance that the delicate tissue of which they are composed is liable to shrivel beyond recognition as the sporangia ripen.

(ii.) *The Occurrence of Periderm in the Sporophylls of* Lepidostrobus oldhamius, *Will.*

In Williamson's original transverse section of *Lepidostrobus oldhamius* ¶ there are distinct indications of a radial arrangement of the cells of the sporophyll lamina towards the dorsal surface. This grouping is sufficiently regular to suggest that periderm is in process of formation. The same appearance of cork at the dorsal surface of the sporophyll lobe occurs in various sections of cones belonging to *L. oldhamius* in Dr. Scott's Collection, *e. g.* S. 1200, a part of a sporophyll from which is shown in transverse section in Pl. **27**. fig. 56.

It seems probable that such cork formation was widely prevalent in the sporophylls of *Lepidostrobus*, since it also occurs in three of the forms described in the present paper—*L. Binneyanus*, sp. nov., *L. gracilis*, sp. nov., and *L. oldhamius* f. *pilosus* (*cf.* Pl. **24**. fig. 20, Pl. **25**. figs. 29 & 36, and Text-fig. 3, B & C). As will be shown on p. 227, the periderm in *L. oldhamius* f. *pilosus* appears to have been hypodermal in origin, and it is not improbable that this was also true in the case of other species. Pl. **25**. fig. 36 represents a transverse section through the dorsal surface of a sporophyll of *L. gracilis*. Here the cork has quite the appearance of being hypodermal. In *L. Binneyanus* also, where the periderm seems at first glance to be epidermal (Pl. **25**. fig. 29), it is possible that the true epidermis may have been discarded.

* Manchester University Coll., Q. 452; Q. 456; Q. 457.

† Williamson, W. C. ('73), p. 295 & pl. 44. figs. 23, 24, 25.

‡ Bower, F. O. ('94), p. 529 & pl. 48. figs. 101 & 102.

§ Brown, R. ('51), p. 471; Bower, F. O. ('94), p. 527 & pl. 48. figs. 96–100; Zeiller, R. ('11), p. 36.

‖ A similar conclusion seems to have been reached by Bower, F. O. ('08), p. 325.

¶ Williamson Coll. Brit. Mus. (Nat. Hist.), C.N. 568.

4. A Description of some New Forms of *Lepidostrobus*.

(i.) Lepidostrobus Binneyanus, sp. nov.

(Pl. 21. fig. 4; Pl. 22. figs. 5–8; Pl. 24. figs. 18–25; Pl. 25. figs. 26–30.)

(1) *Material.*

The Binney Collection, Sedgwick Museum, Cambridge, included, amongst its Lower Coal Measure blocks, one which contained, in addition to other fossils, two cones of a *Lepidostrobus* showing certain peculiar features. A series of sections has now been cut from each of the cones *. The following account is based upon these two fructifications, which may be distinguished as Q. α and Q. β. They appear to belong to species hitherto undescribed, for which I propose the name *Lepidostrobus Binneyanus*.

(2) *General Form and Dimensions of the Cone and Sporophylls.*

We can only arrive at very rough measurements for the cone, owing to the fact that both specimens are fragmentary and much crushed. The fructification was slender, with a diameter of about 1·5 cm., of which the axis occupied 3 mm. The approximate measurements of the upturned limb of the sporophyll are 6 mm. in length and 5 mm. in breadth at the base. It should be remembered, however, that, owing to imperfections of preservation and to distortion of the more delicate parts of the cone, measurements of the length of the upturned limb of the sporophyll of any *Lepidostrobus*, taken from sections of petrified material, are relatively of little value. They are likely to fall considerably below the actual dimensions, and should merely be accepted as minimum measurements. In order to obtain the full measurement, the sporophyll-limb would not only need to be perfectly preserved and uninjured, but the section would require to traverse the whole length of the limb in the median plane, an event which would rarely happen.

In *Lepidostrobus Binneyanus* there was a downward heel at the junction of limb and pedicel, which appears to have sometimes reached a length of about 3 mm. (*l.h.*, Pl. 24. fig. 20). The basal part of the sporophyll lamina was somewhat thick, measuring not less than 1 mm. from dorsal to ventral surface. The sporophyll pedicel, which was 5 to 6 mm. long, was slightly winged (*p.w.*, Pl. 22. fig. 7 and Pl. 25. figs. 26 & 26 *a*), but, owing to the way in which the cones have been crushed, it is exceptionally difficult to determine its exact width. The midrib appears to have been 0·2 to 0·3 mm. wide, while the wing extended on either side for at least 1 mm.

(3) *The Detailed Structure of the Cone Axis.*

The slender xylem cylinder of the cone axis is ·5 mm. (or less) in diameter, and is almost solid (*v.c.*, Pl. 21. fig. 4). There are, however, a few thin-walled pith elements (*p.*) in a central position. These are obliterated by crushing in the transverse section

* Q. α. (1–11) and Q. β. (1–5).

photographed in Pl. 21. fig. 4, but their position can be made out. They are visible in longitudinal section in Pl. 22. fig. 5. The number of tracheides on any radius between the pith and the protoxylem (*px.*) is about four. The contrast in size between the scalariform metaxylem (*mx.*) and the spiral protoxylem elements is unusually great (Pl. 21. fig. 4 and Pl. 24. figs. 18 & 19). The horizontal bars of thickening on the walls of the metaxylem tracheides are connected by delicate vertical striations (Pl. 24. fig. 18). There seems to be a complete or almost complete absence of the short barred tracheides characteristic of the peripheral zone of the xylem in *L. oldhamius*, Will. (*a*)*. The phloem is not preserved. The firm inner cortex (*i.c.*, Pl. 21. fig. 4) is four to five elements in thickness. As is usually the case in *Lepidostrobus*, the middle cortex has perished, but the outer cortex survives.

(4) *The Sporophyll Traces in the Axis.*

We only possess a single radial longitudinal section of *L. Binneyanus*†, and this is somewhat imperfect. The sporophyll traces, as shown in this section, were peculiar in following an obliquely downward path in the outer part of their course from central cylinder to sporophyll (*l.t.*, Pl. 24. fig. 21).

Pl. 24. fig. 22 shows a sporophyll trace, as it appears in transverse section while traversing the space immediately outside the central cylinder. The xylem, which is alone preserved, consists of a compact group of seventeen tracheides; there are two or three small elements occupying a central position which possibly may be the protoxylem. As the sporophyll traces pass through the inner cortex, they each become invested with a sclerised sheath, which accompanies them on their outward journey (*i.c.s.*, Pl. 21. fig. 4 and Pl. 24. fig. 23). As a rule, the xylem alone is preserved, but occasionally a small detached group of elements is also visible on the outer side of the xylem; this may perhaps represent the phloem. The xylem group, which is roughly circular while the trace is still close to the vascular cylinder (Pl. 24. fig. 22), becomes narrowed radially and widened tangentially as it passes further out (Pl. 24. fig. 23). The sporophyll traces in the middle cortical sheath are too much distorted for measurement, but before they become free from the inner cortex their tangential width (including the sheath) is about 0·15 mm.

(5) *The Detailed Structure of the Sporophyll.*

The dimensions and general form of the sporophyll have already been briefly mentioned. A noticeable feature of the winged sporophyll pedicel, when viewed in tangential section, is the occurrence of a cushion of sclerised elements on either side of the median attachment of the sporangium. Many of the cells of the cushion are so thick-walled that their cavities are almost or entirely obliterated (*sc.c.*, Pl. 22. figs. 7 & 8 and Pl. 25. figs. 26, 26 *a*, & 27). On the lower side of the pedicel there is a well-marked keel, of which the histology is somewhat unusual. The epidermal layer (*ep.*) of small cells is succeeded internally by a hypoderma (*hy.*) of large cells with firm walls. These are markedly distinct from the

* Maslen, A. J. ('99), p. 362.

† Q. *a.* 6.

thin-walled cells forming the inner tissue of the keel, which are often much crushed. The epidermis and also the hypoderma seem to consist, in places, of more than one layer of cells; but in spite of this irregularity, the general appearance, as seen in tangential sections, is highly characteristic. It contrasts markedly, for instance, with the large-celled epidermis and absence of hypoderma in *L. oldhamius*, Will., f. *minor* (*cf.* Pl. 22. figs. 7 & 8 with Pl. 26. fig. 40).

The upturned lamina of the sporophyll consists, especially in its basal region, of thin-walled parenchymatous tissue (*l.*, Pl. 22. fig. 6), but sclerenchyma is not altogether absent, and increases in amount higher in the lobe. The appearance of the lamina suggests that it was slightly succulent. The cells towards the dorsal surface are relatively small, and their radial arrangement, as well as the angular form which they assume in cases where the tissue has become crushed or shrunken, indicate that periderm formation has come into play (*pd.*, Pl. 22. fig. 6, Pl. 24. fig. 20, and Pl. 25. fig. 29). There is occasionally a slight appearance of a similar formation at the ventral surface of the sporophyll lamina.

An interesting feature is the occurrence of delicate cellular outgrowths (*l.o.*, Pl. 22. fig. 6 and Pl. 25. fig. 30), which appear to arise from the inner surface of the downward heel (or dorsal flap) which occurs at the base of the sporophyll lamina. Unfortunately the preservation is not sufficiently perfect to make it possible to give an exact account of the nature and arrangement of these structures. However, from a comparison of the two sections in which they can be distinguished, I am inclined to think that they consisted of cell-plates, two or three elements in thickness.

The anatomy of the sporophyll trace during its passage through the pedicel is illustrated in Pl. 22. fig. 8 and Pl. 25. fig. 28. The small compact xylem group, consisting, in three cases in which the elements were counted, of less than a dozen tracheides, is surrounded by large transfusion elements, which are especially abundant on the upper side of the bundle. These transfusion tracheides are very well developed at the junction of lobe and pedicel. In the upturned lobe, the bundle presents the same general appearance as in the pedicel, but the tracheides are fewer in number.

(6) *The Ligule.*

A ligular pit is visible in more than one case, and the body marked "? *lg.*" in Pl. 24. fig. 20, may perhaps represent the ligule itself.

(7) *The Sporangium.*

The sporangium has the radially elongated attachment to the pedicel, which is one of the characteristics of the genus *Lepidostrobus*. The distal and proximal ends of the sporangial base are represented in Pl. 24. figs. 20 & 21. The attachment is of considerable breadth, and a massive ridge of tissue is continued up into the base of the sporangial cavity (*st.r.*, Pl. 22. fig. 7, Pl. 24. fig. 21, and Pl. 25. figs. 26 & 27). This may perhaps be interpreted as of the nature of sterilised sporangial tissue, since it is bounded on either side by a continuation of the sporangium wall *, but, at the same time, it is perfectly continuous with the parenchyma of the sporophyll.

* Maslen draws attention to the same feature in the case of *L. oldhamius* (β) and *L. foliaceus*. Maslen, A. J. ('99), pp. 370 & 374, pl. 38. figs. 32 & 38.

The cells, which compose the sterile ridge, are often somewhat elongated in a vertical direction. The most interesting feature of the tissue is that, in some cases, the walls of these elongated cells are marked by delicate bars of thickening, indicating that they were transfusion elements (Pl. 25. fig. 27). The distribution of these elements seems to be very irregular. In certain tangential sections none can be detected (*e. g.*, the one represented in Pl. 25. fig. 26 *a*), in others there are a few, while in others again (*e. g.*, Pl. 25. fig. 27), the tissue of the ridge appears to be almost entirely composed of such elements, which are continuous below with the transfusion tracheides of the sporophyll pedicel.

The sporangia, as seen in tangential section, are much crushed and distorted, dehiscence having already taken place. The structures inside the sporangium are hence difficult to interpret, but there are indications of the existence of an outgrowth of cellular tissue arising from the sterile ridge and penetrating into the cavity of the sporangium (*st.p.*, Pl. 25. fig. 27).

The sporangium wall is of the usual columnar type (Pl. 25. figs. 26 *a*, 37, & 38), lined internally by a narrow zone of delicate thin-walled tissue which is poorly preserved.

(8) *The Spores.*

The spores are somewhat more mature in Q. β. than in Q. α. In the former cone they are often still arranged in tetrads (Pl. 24. fig. 24). The ripe spores show the triradiate marking with great distinctness, and the wall is also decorated with a narrow wing in the equatorial plane (Pl. 24. fig. 25). The greatest diameter of the spores is about ·03 mm , showing that the cone was either homosporous or microsporangiate.

(9) *Comparison with other Species of* Lepidostrobus.

The cone of *Lepidostrobus Binneyanus* is considerably smaller in diameter than that of the type form of *L. oldhamius* * or *L. Bertrandi* †. It also differs from *L. oldhamius* in having no well-marked groove on the outer surface of the sporophyll lamina at its junction with the heel ‡. The tangential width of the sporophyll trace, including its sheath, just as it emerges from the inner cortex, is 0·15 mm. This is similar to the corresponding dimension in the case of *L. oldhamius*, Will. (α) of Maslen §, but slightly less than that of the type form of *L. oldhamius*; in the case of one of the original sections of the latter figured by Binney ‖, I have found the sporophyll traces in this region to be about 0·25 mm. in diameter. From *L. Bertrandi*, *L. Binneyanus* also differs anatomically in possessing a strongly thickened inner cortex, and in having delicate vertical striations between the horizontal thickening bars of the scalariform tracheides (Pl. 24. fig. 18).

* The diameter of *L. oldhamius*, measured from sections 87 and 88, Binney Collection, Sedgwick Museum, is about 3 cms.

† The cone of *L. Bertrandi* is as much as 5 cms. in diameter. See Zalessky, M. ('08), p. 33.

‡ Compare Pl. 24. fig. 20 of the present paper with Seward, A. C. ('10), fig. 191 B, p. 188. Maslen's restoration of the type form of *L. oldhamius* fails to show this characteristic groove, Maslen, A. J. ('99), pl. 37. fig. 22.

§ Maslen, A. J. ('99), p. 364.

‖ Binney Coll., Sedgwick Museum, Cambridge, Section 88, figured Binney, E. W. ('71), pl. 7. figs. 2, 4, 5.

It further differs both from *L. oldhamius* and *L. Bertrandi* in its extremely small pith, and in the fact that the sporangium is attached to the upper surface of the pedicel by a well-marked longitudinal ridge, which may possibly represent a sterilised region of the sporangial tissue (*st.r.*, Pl. 22. fig. 7, Pl. 25. figs. 26, 26 *a*, & 27). In this feature, as well as in the occurrence of sclerised lateral pads (*sc.c.*) on the upper surface of the pedicel, it approaches *L. foliaceus*, Maslen *, from which, however, it differs in various important points. The cone is larger than that of *L. foliaceus*, and the laminæ of the sporophylls are not constricted at the base, and do not consist of the large-celled parenchyma with secretory cells which is so characteristic of *L. foliaceus*.

The small, fragile cone of *L. Binneyanus* belongs, obviously, to an entirely different type from the massive fructification of the Lower Carboniferous *L. Brownii*, with its cushion-like sporophyll lobes. It resembles it, however, in one feature, namely that the sporophyll trace is accompanied, apparently throughout the entire length of the pedicel, by transfusion tracheides †, which are especially abundant on the ventral side (Pl. 22. fig. 8, Pl. 24. fig. 20, Pl. 25. fig. 28).

In addition to the characters, to which we have just referred, in which *L. Binneyanus* resembles one or other of the known species of *Lepidostrobus*, this cone also shows certain features which cannot be paralleled in any member of the genus hitherto described. The sporophyll pedicel is more broadly winged than that of any other *Lepidostrobus* known to us in the petrified state (Pl. 25. fig. 26), though these wings sink into insignificance when they are compared with those of various so-called "bracts" of *Lepidostrobus*, which occur as impressions ‡. As regards internal structure, a highly characteristic feature is the histology of the keel of the pedicel, which is notable for the large-celled hypoderma which is situated beneath the small-celled epidermis (Pl. 22. figs. 7 & 8). The occurrence of abundant transfusion elements in the ridge of sterile tissue which forms the floor of the sporangium (Pl. 25. fig. 27), is also a character which has not been recorded for any other Upper Carboniferous species.

Another point, in which *L. Binneyanus* appears to be unique, is the course of the sporophyll traces, which pursue an obliquely downward path in the outer part for their journey from vascular cylinder to pedicel (Pl. 24. fig. 21). While this arrangement differs from that which prevails in the other species of *Lepidostrobus*, in which, as is well known, the traces pass obliquely upwards from stele to sporophyll §, it recalls the anatomy of *Mesostrobus* ‖.

(10) *Diagnosis.*

LEPIDOSTROBUS BINNEYANUS, sp. nov.

Horizon. Lower Coal Measures.

Cone slender, about 1·5 cms. in diameter, with axis 3 mm. in diameter.

* Maslen, A. J. ('99), p. 373 & pl. 38. figs. 36–39.

† Zeiller, R. ('11), p. 32.

‡ *L. fimbriatus.* See Kidston, R. ('83), pl. 31. figs. 2, 3, 4.

§ Williamson, W. C. ('94), pl. 6. fig. 62; Zalessky, M. ('08), pl. 3. figs. 1 & 1 *a*; Bower, F. O. ('93), p. 339.

‖ Watson, D. M. S. ('09), text-fig. 1, p. 381.

Vascular cylinder of cone-axis containing a very small pith.

Metaxylem tracheides scalariform, with delicate vertical striations between the bars of thickening.

Sporophyll traces follow an obliquely *downward* direction in the distal portion of their course from stele to sporophyll pedicel. The bundle is accompanied by transfusion tracheides throughout the pedicel.

Sporophyll pedicel about 6 mm. in length, *winged*, with a *sclerised ridge* on either side of the median line. The pedicel has a *keel* which is characterised by an epidermis of small cells, followed internally by a large-celled *hypoderma*.

Sporangium attached to pedicel by means of a well-marked ridge of tissue, containing *transfusion elements*. There appears to be a *radial plate of sterile tissue* arising from the floor of the sporangium.

Spores about 0·03 mm. in diameter, including the equatorial border.

(ii.) Lepidostrobus gracilis, sp. nov.

(Pl. 22. fig. 9; Pl. 23. figs. 10–12; Pl. 25. figs. 31–39; Pl. 26. figs. 40–42.)

(1) *Material.*

The material on which the following account is based consists primarily of five sections* (four longitudinal and one transverse) cut from coal-balls obtained by Mr. Lomax from Hough Hill, Stalybridge. Two of these sections† were cut from the same cone, and the three others, though cut from different cones, appear to belong to the same type.

A single section in the Williamson Collection, British Museum (C. N. 1776 D.), which is described in Williamson's manuscript catalogue as "an apparently distinct form," seems also to belong to this species. In addition, the Leiden Herbarium possesses a series of sections‡, including considerable portions of two cones, which are probably specifically identical with *L. gracilis*. These latter cones were obtained from the Seam Fine Frau-Nebenbank, Rheinpreussen Colliery, near Duisburg, Germany.

(2) *General Form and Dimensions of the Cone and Sporophylls.*

Some idea of the general construction of the strobilus may be obtained from the photograph reproduced in Pl. 23. fig. 10, which is tangential as regards the middle region, but nearly radial at the sides. In the two principal longitudinal sections, the cone is incomplete at the apex§ and possibly at the base also. The dimensions of the longest fragment are 4·6 cms. in length by 0·9 cm. in diameter, but, as there is no truly radial section, the actual width of the cone must be estimated as

* Slides 276, 277, 278, 279, 280, Sedgwick Museum Coll., Cambridge.

† Slides 276 & 277.

‡ Slides C 1, C 1 *g* 1–5, *g* 10–16, Leiden Herbarium Coll.

§ Slide C 1, *g* 1, Leiden Herbarium Coll., shows the apex of a cone which appears to belong to this species. It is acutely pointed and formed of overlapping sporophyll laminæ. The sporophyll pedicels towards the tip of the cone leave the axis at an acute angle, whereas, in the main part of the cone, they leave it almost at right angles.

somewhat greater than would appear from these measurements. It is clear that, even allowing for the full width not being seen in the sections available, the fructification was unusually slender in proportion to its length. The pedicel, which was not less than 4 mm. long, was about 1 mm. in width near the axis, and slightly broader further out. The lamina appears to have attained a length of 12 mm. or more, with, in addition, a downward keel 2 mm. in length. None of the preparations are truly radial and the apices of the sporophylls are, as a rule, either not preserved or missed in the sections, with the result that a superficial examination would lead one to suppose that the lamina was only about 5 mm. in length. The width of the sporophyll at the level of insertion of the ligule was about 6 mm. It will be recognised from this description that the sporophyll, if found as a detached object in "impression material," would closely resemble one of the spade-like examples of *Lepidophyllum* with their narrow pedicels, such as *L. brevifolium*, Lesq., which has recently been recorded from the British Coal Measures *.

(3) *The Detailed Structure of the Cone Axis.*

Our knowledge of the anatomy of the cone axis is derived from a single transverse section. The axis was traversed by a vascular cylinder enclosing a pith (Pl. 23. figs. 11 & 12). The cylinder is small, its diameter being about 0·3 mm. Between the protoxylems and pith there are, on any radius, 3 to 4 large xylem elements. A marked characteristic of the axis is that the outer zone of the inner cortex (*i.c.*) is formed of darker and more resistant tissue than the corresponding zone in the type specimens of *Lepidostrobus oldhamius*. The middle cortex is absent, and the firm outer cortex is of the usual type.

(4) *The Sporophyll Traces in the Axis.*

The preservation is not sufficiently good to allow the number of sporophyll traces, cut across in a transverse section of the axis, to be determined with certainty, but it is clear that they were relatively few, probably not more than 20.

Sporophyll traces, just on the point of leaving the axis, are shown in tangential section in Pl. 25. fig. 31. Each is accompanied by a large parichnos space. The trace consists of a mass of xylem, in which no protoxylem can be recognised with certainty, and a ventral crescent of "phloem," separated from the xylem by a zone of parenchyma (Pl. 25. fig. 34). The "phloem" evidently consisted of delicate thin-walled cells, for it has suffered almost complete destruction. There are no transfusion elements in this region.

(5) *The Detailed Structure of the Sporophyll.*

Near the axis of the cone the pedicel is triangular in section, without an elongated dorsal keel (Pl. 25. figs. 31 & 32). In this region it is composed, externally, of several layers of dark, thick-walled cells, followed internally by a thin-walled zone, surrounding the parichnos space (*par.*). The vascular bundle is embedded in this thin-walled tissue

* Arber, E. A. N. ('12), p. 252.

on the ventral side of the pedicel. Enclosed in a sheath of this tissue, it protrudes into the parichnos space, which becomes reniform when seen in tangential section.

Further from the axis, the pedicel widens to about 1·5 mm., the triangular form becomes slightly modified, and the parichnos space disappears (Pl. 25. fig. 33 and Pl. 26. fig. 40). A very short dorsal keel is developed, and the dark sclerised tissue becomes concentrated into two ventral cushions (*sc.c.*) lying to right and left of the attachment of the sporophyll. Transfusion tracheides do not occur in the proximal region of the pedicel, but they are abundant towards the distal end (Pl. 25. fig. 35) and in the upturned limb (Pl. 26. fig. 42).

The sporophyll thickens considerably, where the lamina joins the pedicel, and the upturned portion appears to have a thick median rib. In the sporophyll lamina the tissue on the outer or dorsal side is dark and resistant, while that on the ventral side, which includes the bundle, consists of thin-walled cells. The arrangement of the cells near both surfaces of the lamina suggests that periderm formation may have occurred here to a slight extent (Pl. 25. fig. 36).

(6) *The Ligule.*

A ligule is seen in one case in transverse section. It is enclosed in a ligular pit, and its attachment is shown (Pl. 26. fig. 41).

(7) *The Sporangium.*

The sporangium is attached to the pedicel by a slender median ridge of tissue which rises into the cavity of the sporangium (*st.r.*, Pl. 25. fig. 33 and Pl. 26. fig. 40). This ridge is bounded laterally by the wall of the sporangium, and may perhaps, as in *L. Binneyanus*, be regarded as consisting of sterilised sporangial tissue (see p. 214). Since dehiscence has taken place, it is difficult to examine the structures inside the sporangium, but there is no doubt that an upgrowth of sterile tissue of plate-like form arose from the floor of the sporangium (*st.p.*, Pl. 25. fig. 33).

The outer cells of the sporangial wall are of the usual columnar type, and sometimes one or two layers of thin-walled cells are preserved internal to them. The columnar layer is thicker where it approaches the supporting pedicel (Pl. 25. fig. 37 *b*) and thinner on the ventral side (Pl. 25. fig. 37 *a*). Dehiscence took place by means of a longitudinal split along the median line of the upper surface (Pl. 25. fig. 32).

(8) *The Spores.*

Very few of the spores are retained, since the preparations are from cones that have already dehisced. Some of the spores are shown in Pl. 25. fig. 39. They are slightly bordered in the equatorial plane. Their maximum diameter is about 0·028 mm.

(9) *Comparison with other Species of* Lepidostrobus.

The cone of *Lepidostrobus gracilis* is more slender in form than that of any other member of the genus hitherto described as a petrifaction. The diameter is less than 1 cm., even in the case of a cone which was certainly mature, as most of the sporangia

have dehisced. The number of sporophyll traces cut across in a single transverse section of the axis does not appear to exceed 20, whereas in the forms of *Lepidostrobus oldhamius* described by Maslen * the number ranges from 30 to 60. This difference is no doubt correlated with the small dimensions of the axis in *L. gracilis*. The ligule, or at least its base, is sunk in a definite ligular pit (Pl. 26. fig. 41), while, according to Maslen †, "the complete absence of a ligular chamber" characterises *L. oldhamius*. The structure of the sporophyll pedicel also differs from that of *L. oldhamius*, and more closely recalls that of *L. foliaceus* ‡ and *L. Binneyanus* § in possessing two lateral, sclerised cushions, between which the sporangium is attached by means of a ridge of sterile tissue. In the details of its histology, however, the pedicel differs markedly from that of *L. Binneyanus* (see p. 213), while the lamina differs no less widely from that of *L. foliaceus* with its large-celled parenchyma and secretory cells.

(10) *Diagnosis.*

LEPIDOSTROBUS GRACILIS, sp. nov.

Horizon. Lower Coal Measures.

Cone very slender in proportion to its length; about 1 cm. in diameter.

Vascular cylinder of cone axis about 0·3 mm. in diameter, enclosing a pith.

Outer zone of inner cortex, a resistant, dark-coloured tissue.

Sporophyll pedicel about 4 mm. in length. Short dorsal keel and a ventral sclerised cushion on either side of the median line.

Sporophyll lamina not less than 12 mm. in length. Tissue dark and resistant towards the dorsal surface.

Ligule sunk in a ligular pit, at least as regards its base.

Sporangium attached to the pedicel by a slender median ridge of tissue, which is carried up into the cavity of the sporangium as a sterile plate.

Spores, diameter about 0·028 mm., slightly bordered in the equatorial plane.

(iii.) LEPIDOSTROBUS OLDHAMIUS, Will., f. MINOR.

(Pl. 23. figs. 13 & 14; Pl. 26. figs. 43–49.)

(1) *Material.*

One of the Lower Coal Measure blocks in the Binney Collection, Sedgwick Museum, contained a cone which, although it bears a general resemblance to *Lepidostrobus oldhamius*, Will., yet diverges from it sufficiently to entitle it to rank at least as a "form" of this species. The cone has been cut up into five longitudinal sections ‖, of which Pl. 23. fig. 13 represents a typical example.

* Maslen, A. J. ('99). † Maslen, A. J. ('98), p. 259.

‡ Maslen, A. J. ('99), p. 374, and pl. 38. figs. 37 & 38.

§ See Pl. 22. fig. 7 and Pl. 25. figs. 26 & 27 of the present paper.

‖ Binney Coll., Sedgwick Museum, AM. (25–29).

(2) *General Form and Dimensions of the Cone and Sporophylls.*

The specimen consists of the apical portion of a cone of which the base has been destroyed, so that it is impossible to determine the dimensions of the fructification as a whole. The length of the existing fragment is nearly 2·5 cms. The sporophylls to one side are slightly damaged; if they were complete the greatest diameter would be 1·5 cms. The axis is 3 to 4 mm. in width. The apices, both of the cone as a whole and of the axis, are noticeably obtuse and rounded. The laminæ of the sporophylls curve over and protect the apex (Pl. 23. figs. 13 & 14).

The sporophylls spring from the axis at an angle very slightly less than a right angle (Pl. 23. fig. 13 and Pl. 26. fig. 43). It should be recalled, however, that the angular relation of sporophyll to axis may vary in different regions of the same cone. We are here dealing only with the apical part of the strobilus, so it is unsafe to lay much stress on this character. The laminæ of the sporophylls are relatively short. The pedicel is nearly 6 mm. long and apparently from 1–2 mm. wide, whereas the upturned part of the lamina seems to be only 3–4 mm. long, and the downward heel about 1 mm. The width of the lamina appears to have been 3–4 mm., but the absence of transverse sections makes it impossible to check the accuracy of this statement. The uncertainty connected with measurements of the sporophyll in petrified material has been referred to on p. 212, but it is at least clear that in this case as in *Lepidostrobus gracilis*, it was of the "spade" type, without a broadly winged pedicel. In *L. oldhamius* f. *minor* the pedicel appears to be longer and the lamina smaller than in *L. gracilis*.

(3) *The Cone Axis.*

The detailed structure of the cone axis cannot be ascertained, owing to the absence of transverse sections and to the fact that in the longitudinal sections the vascular cylinder is not in any case preserved. The outer cortex consists of the usual elongated cells with firm walls.

(4) *The Sporophyll Traces in the Axis.*

On examining the section which is photographed in Pl. 23. fig. 13, the outgoing sporophyll traces are found to be cut almost *longitudinally*, although the outer cortex is traversed *tangentially*. This indicates that the course of the sporophyll traces, at least in the outer region of the axis, was markedly steep.

(5) *The Detailed Structure of the Sporophylls.*

The sporophyll pedicel is triangular in section, and the dorsal keel is scarcely developed (Pl. 23. fig. 14 and Pl. 26. figs. 46 & 47). There are slightly raised sclerised cushions on the ventral surface to right and left of the median line. The outer layers of the pedicel consist of thick-walled sclerised tissue, and the inner thin-walled zone is not preserved. The result is that the parichnos appears to be larger than it was during

life; the space occurs throughout the pedicel and occupies part of the heel of the lamina (Pl. 26. fig. 43).

When the pedicel leaves the axis, the xylem portion of its trace consists of 16 or more elements. There seems to be a tendency for the smaller elements (? protoxylem) to be placed internally towards the ventral side of the bundle. The general structure of the pedicel is clearly shown in the case of some sporophylls bearing young or abortive sporangia, which are cut tangentially near the apex of the cone (Pl. 26. fig. 47). In the region of the junction of pedicel and lamina, the bundle is accompanied by a considerable mass of large transfusion tracheides. These lie chiefly on the ventral side, but a few occur on the dorsal side (Pl. 26. fig. 44) and also on the flanks of the bundle.

In the upturned part of the lamina the outer tissues are dark in colour and appear to consist of thick-walled cells, but the bundle traverses a clear-looking, parenchymatous, central zone. The bundle is accompanied by transfusion tracheides for some distance up the lamina on the ventral side. The epidermis on the inner face of the lamina forms a particularly well-marked layer.

(6) *The Ligule.*

A ligule and a narrow ligular pit appear to be preserved in the case of one sporophyll (Pl. 26. fig. 45).

(7) *The Sporangium.*

The sporangium is attached directly to the upper surface of the pedicel, without the intervention of a ridge of sterilised sporangial tissue. There is, however, a delicate radial plate of sterile tissue rising into the cavity of the sporangium (*st.p.*, Pl. 26. fig. 46). The distal wall of the sporangium slopes sharply backward from the region of its attachment to the pedicel, thus leaving a considerable space between the upturned limb of the sporophyll and the end of the sporangium (Pl. 26. fig. 43). The sporangium wall consists of an outer layer of columnar dark cells followed internally by one or two layers of thin-walled cells. In Pl. 26. fig. 48 these two regions of the wall are seen in succession in an obliquely tangential section.

(8) *The Spores.*

The sporangia contain spores whose greatest diameter is 0·028 to 0·03 mm., from which we may infer that the cone was microsporangiate or homosporous. Some of the spores are shown in Pl. 26. fig. 49. They were bordered in the equatorial plane and the triradiate marking is particularly distinct.

(9) *Comparison with other Forms of* Lepidostrobus oldhamius, *Will.*

It seems clear that the cone under discussion cannot be assigned to the type form of *L. oldhamius*. It differs therefrom in its relatively small size, in the backward slope of the distal walls of the sporangia (Pl. 26. fig. 43), which show no tendency to curve over

and hide the region of insertion of the ligule, and in the absence of a groove on the dorsal surface of the sporophyll between lamina and heel. The absence of any pad of sterile tissue on the floor of the sporangium, and the presence of a ridge of sclerised tissue to right and left of the median line of the sporophyll pedicel, in place of fairly uniform sclerisation, are other characters which distinguish *L. oldhamius* f. *minor* from the type form.

It is possible, however, that this cone may eventually prove to be identical with Maslen's *L. oldhamius* (*a*).* The two cones agree in the diameter of the axis and apparently also in the number of xylem elements which pass into the sporophyll trace. *L. oldhamius* f. *minor* is somewhat more slender than *L. oldhamius* (*a*), but this may be due to the fact that in the former case we possess only the apical part of the cone, whereas in *L. oldhamius* (*a*) the apex is unknown. It is impossible, however, to compare *L. oldhamius* (*a*) and *L. oldhamius* f. *minor* in detail because, in the specimens described under the former title, the structures outside the axis have scarcely survived, while, in the latter, the sporophylls and sporangia are well preserved, though nothing can be seen of the internal structure of the axis.

(iv.) Lepidostrobus oldhamius, Will., f. pilosus.

(Plate 27. figs. 50–54; Text-figs. 2, 3 (A, B, & C), 4.)

(1) *Material.*

The British Museum (Nat. Hist.) possesses a single section of a cone from Oldham (V. 8871, General Collection) which Williamson † figured, and to which he devoted a few lines of description. This section shows remarkable resemblances to two cones from Shore, Littleborough, preparations of which are included in the collections belonging to University College, London, to Manchester University, and to Mr. D. M. S. Watson. The seven transverse sections in the University College and Watson Collections have obviously been cut from the same cone, which, for purposes of description, we may distinguish as Cone A. Taken in the following order they form a series passing downwards from the apex of the cone:—U. C. L., C. 16. *d*; Watson, A. 92; U. C. L., C. 16. *c*; Watson, A. 93; U. C. L., C. 16. *b*; Watson, A. 94; U. C. L., C. 16. *a*. A set of transverse sections of a second cone, which we may call Cone B, is preserved in the Manchester University Collection. The following is the order of the sections from the apex of the cone downwards:—R. 387; R. 386. *b*; R. 386. *a*; R. 385. *b*; R. 385. *a*. In both A and B the extreme top of the fructification is preserved, but A is the more complete, since it includes a lower region of the cone than is seen in B. Cones A and B and the Williamson section referred to above resemble *Lepidostrobus oldhamius*, but they have, at the same time, certain peculiar features which seem to render it advisable to distinguish them in some way. For this purpose I propose to use the provisional name *Lepidostrobus oldhamius*, Will., f. *pilosus*.

* Maslen, A. J. ('99), p. 361.

† Williamson, W. C. ('94), pl. 8. fig. 56, & p. 27.

(2) *General Form and Dimensions of the Cone and Sporophylls.*

As no longitudinal sections are known, it is impossible to estimate the length of the cone. The maximum diameter of the whole fructification was about 2 cms. and of the axis about 4 mm. However, as no specimens are at present available showing the base of the cone, it is probable that these numbers do not give the full dimensions.

Towards the apex the cone was of tapering form, and the laminæ of the sporophylls extended for some distance above the tip of the axis. Numerous laminæ are shown in Pl. 27. fig. 52 which passes through the apex of a cone. The outline of the apex, as seen in transverse section, was rendered irregular by the very prominent bases of the sporophyll pedicels (Pl. 27. fig. 50). The vertical height of the sporangia must have been extremely small, since a very slight obliquity in a transverse section—so slight as to be scarcely recognisable in the case of the axial region—is sufficient to make the sporangia appear almost as in tangential section, with the pedicel proximally placed on one side of the cone and distally placed on the other side (*cf.* the sporangia to the upper right-hand side and the lower left-hand side of the photograph, Pl. 27. fig. 50).

The width of the sporophyll lamina at the level of insertion of the ligule is 7 mm. The length of the lamina must have been considerable, judging by the number of overlapping sporophylls seen outside the sporangia in any transverse section. The unusual development of the sporophyll laminæ is the only feature of this cone to which Williamson's description draws attention. He remarks on the "well defined sections of the overlapping free ends of the sporangiophores, which have somewhat the form of similar sections of leaves of *Lepidophloios*" *, and points out that they are more foliaceous than those of *Lepidostrobus Brownii*.

(3) *Detailed Structure of the Cone Axis.*

The xylem cylinder of the cone axis does not exceed 0·7 mm. in diameter. It has a large pith, 0·45 mm. across. The xylem is peculiar in including a relatively small number of metaxylem elements. Williamson does not figure or mention the vascular cylinder, but on examining the section † which he describes, I have found that there is no metaxylem present, only the protoxylem being developed. The lowest section of Cone A ‡ is the one in which we should expect to find the xylem at its fullest development, since it is cut further from the cone apex than any other section of the species which we possess, but even here the metaxylem is interrupted at intervals, and does not form a continuous hollow cylinder, whereas the small elements of the protoxylem external to it are arranged in an unbroken sheath (Pl. 27. figs. 50 & 51). The pith, which survives in more than one section, consists externally of delicate collenchymatous elements and internally of larger cells with firmer walls.

The inner cortex, when it is preserved, forms a narrow zone of thin-walled cells (*i.c.*, Pl. 27. fig. 51). The outer cortex is a firm layer, which may reach a thickness of about 0·7 mm. between the leaf bases (*o.c.*, Pl. 27. fig. 50).

* Williamson, W. C. ('94), p. 27.

† Brit. Mus. (Nat. Hist.) General Collection, V. 8871.

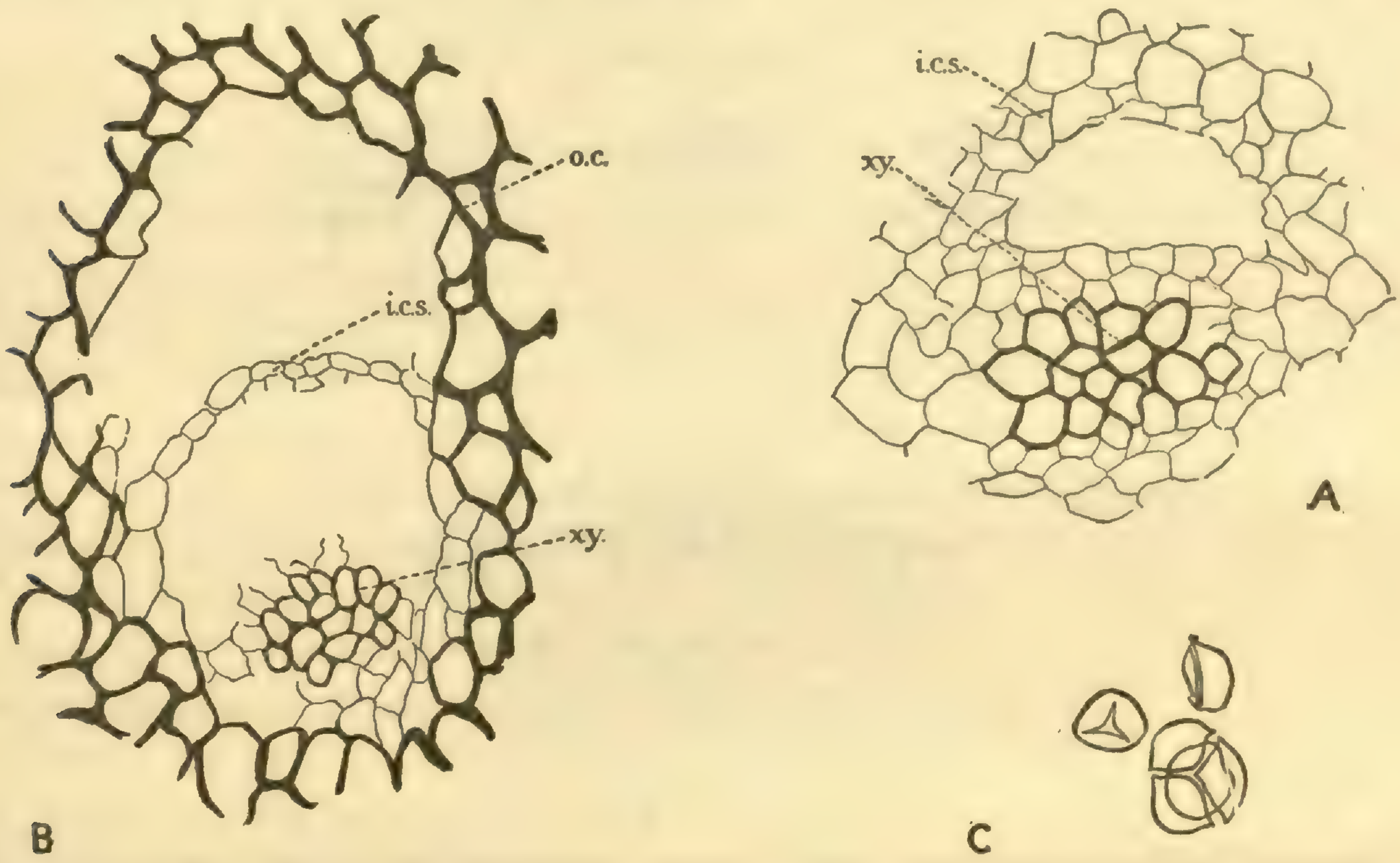
‡ U. C. L. Coll., C. 16. *a*.

The great interest of the anatomy of the cone axis of this species lies in the variations in structure which arise as the apex is approached. This point will be dealt with more fully in Section 5 of the present paper (see pp. 228–230 and Text-fig. 4).

(4) *The Sporophyll Traces in the Axis.*

Numerous sporophyll traces are visible in the transverse sections. In one case * I have counted about 50. The xylem of these traces is fairly massive; immediately after

Text-fig. 2.



Lepidostrobus oldhamius, Will., f. *pilosus*.

A. Sporophyll trace in middle cortex, from a transverse section of the cone axis. *Watson Coll.*, A. 94. (×318.)

B. Sporophyll trace in outer cortex, from a transverse section of the cone axis. *Watson Coll.*, A. 93. (×318).

(*xy.* = xylem; *i.c.s.* = inner cortical sheath; *o.c.* = outer cortex.)

C. A tetrad of spores and two single spores, one of which shows the triradiate marking and the other the equatorial border. *U. C. L. Coll.*, C. 16. *b*. (×318.)

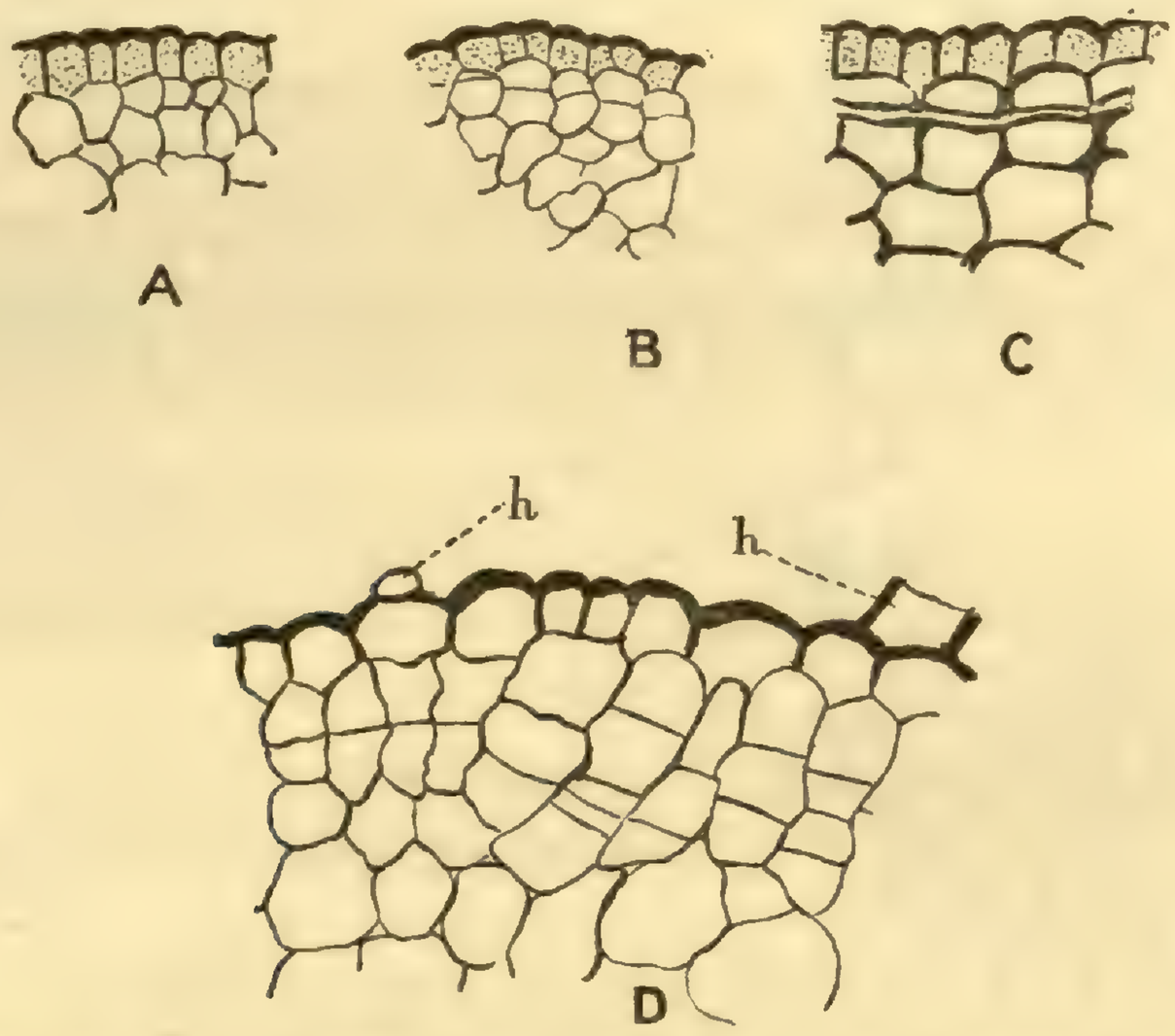
leaving the central cylinder it consists of 14 to 19 tracheides. As usual, the bundles acquire a sheath of delicate tissue in passing through the inner cortex. The diameter of sporophyll trace and sheath while in the middle cortical space is 0·15 to 0·18 mm. Traces from the middle and outer cortical regions respectively are shown in Text-fig. 2, A & B. Near the cone apex the inner cortex is no longer differentiated, and in consequence the sporophyll traces possess no sheath.

* U. C. L. Coll., C. 16. *b*.

(5) *The detailed Structure of the Sporophyll.*

Owing to the absence of longitudinal sections it is difficult to elucidate the structure of the sporophyll pedicel. Some of the transverse sections, which are slightly oblique, show, however, that the pedicel bore two lateral sclerised pads. The sporophyll trace consisted as usual of spiral tracheides. Transfusion elements can occasionally be recognised in the neighbourhood of the bundle not far from the proximal end of the pedicel, but they do not become abundant until the distal end is approached. At the base of the upturned lobe of the sporophyll the transfusion tracheides are large and conspicuous,

Text-fig. 3.



A and B. *Lepidostrobus oldhamius*, Will., f. *pilosus*. Part of the dorsal surfaces of two sporophylls from a transverse section traversing the sporophylls above the apex of the cone axis. A is from a very young sporophyll in which no periderm has yet developed. B is from an older sporophyll, in which there are indications of hypodermal periderm. *Manchester University Coll.*, R. 387. (×258.)

C. *Lepidostrobus oldhamius*, Will., f. *pilosus*. Part of the dorsal surface of a sporophyll lamina from a transverse section through the sporophyll at the level of the ligule. *U. C. L. Coll.*, C. 16. *a*. (×258.) Apparently a hypodermal periderm is just being initiated, and cracking has occurred during petrifaction along the plane of weakness caused by the first formed walls.

D. *Paulownia imperialis*, S. & Z. (Scrophulariaceæ). Part of dorsal surface of a calyx segment in transverse section to show hypodermal periderm for comparison with figs. B & C. (×258.) (*h* = base of a hair.)

and they remain so throughout the entire length of the lamina. Here they form a discontinuous sheath surrounding the small xylem group, but generally placed at some little distance from it.

The lamina was flat and leafy, becoming narrower and thicker towards the tip, where it was almost triangular in section. In the apical region the tissue was darker and more sclerotic than at a lower level. An interesting feature was the remarkable hairiness of the very young sporophyll laminæ. The hairs, which are shown in Pl. 27. fig. 53, arose

from the epidermis of both dorsal and ventral surfaces of the young laminæ, and formed a tangled mass filling the spaces between the sporophylls. They are of considerable size, varying in diameter from 0·014 to 0·025 mm. Their length cannot be estimated, as they are so much curved and twisted that any section cuts them into numerous segments, but since no septa can be detected, it is probable that they were unicellular. These hairs appear to have been most abundant in the basal region of the laminæ. They were ephemeral structures, disappearing in the case of the older sporophylls; those growing from the lateral margins were retained longest. The hairs are so noticeable a feature that I propose, on their account, to distinguish these cones as *Lepidostrobus oldhamius*, Will., f. *pilosus*.

The sporophylls of *L. oldhamius* f. *pilosus* throw considerable light upon the origin of the periderm, which, as I have shown on p. 211, commonly occurs in the cone scales of this genus. In this connection one of the sections † of Cone B in the Manchester University Collection is particularly valuable, since it traverses the apex of the cone above the tip of the axis, and provides a series of transverse sections of sporophylls. Those in the centre are quite young, but in passing towards the periphery of the section, we meet with progressively older examples. The younger sporophylls are bounded, both dorsally and ventrally, by a very distinct and regular epidermis. In the older sporophylls, on the other hand, the dorsal surface is protected by a layer of periderm. A comparison of such stages as those represented in Text-fig. 3, A & B, renders it highly probable that the phellogen was hypodermal in origin. This suggestion is confirmed by an examination of Cone A. Here, in a transverse section ‡ which passes through the base of a sporophyll lamina at the level of the ligule, we meet with an appearance (Text-fig. 3, *c*) which exactly suggests, at first sight, an early stage in the development of hypodermal periderm in various modern plants. It is possible, however, that the diagrammatic character of this section may be a little deceptive, and that the apparent tangential strip of "phellogen" may be due merely to the separation of the cell-walls, owing to splitting during or before petrifaction. But even if this is so, the crack probably followed the plane of weakness of the earliest walls which were laid down when periderm formation was initiated. As an example, from the Phanerogams, of a similar formation of cork for the protection of the reproductive organs, we may take the hypodermal periderm, which is developed in the sepals of the Scrophulariaceous tree, *Paulownia imperialis*, Sieb. & Zucc., even before the flower-buds begin to unfold (Text-fig. 3, D).

(6) *The Ligule.*

In one of the transverse sections § cut near the cone apex six ligules are visible (*lg.*, Pl. 27. fig. 54). The immaturity of this region of the cone no doubt accounts for the preservation of so large a number of these organs.

* These hairs may be compared with those occurring at the base of the sporophyll pedicel in *L. Brownii*. Zeiller, R. ('11), pl. 13. figs. 7–9.

† Manchester University Coll., R. 387. Figured as a low power drawing, Seward, A. C. ('10), fig. 189, p. 184.

‡ U. C. L. Coll., C. 16. *a*.

§ Manchester University Coll., R. 386. *b*.

(7) *The Sporangium.*

The extreme tangential width of the sporangium is 3 mm. and its radial length is 5 to 6 mm. As already pointed out, it appears to have been shallow in its vertical dimension. A pad of sterile tissue occupies the floor of the sporangium, and from this a plate-like process arises into the cavity in the median plane. The sporangium wall consists of the usual columnar outer layer, with a lining of soft tissue.

(8) *The Spores.*

The spores are about 0·023 mm. in diameter. They have a narrow border in the equatorial plane, and in some cases the characteristic triradiate marking is visible (Text-fig. 2, C).

(9) *Comparison with other forms of* Lepidostrobus oldhamius, *Will.*

The dimensions of the whole cone, the axis, the vascular cylinder, and the sporophyll traces of *L. oldhamius* f. *pilosus* agree closely with those of the form which Maslen* distinguishes as *L. oldhamius*, Will. (*a*). It differs from the latter, however, in several respects. The number of xylem elements in the sporophyll traces is somewhat greater, and the traces cut across in any given transverse section are more numerous. The thick continuous zone of protoxylem, the relatively small amount of metaxylem, and the absence of peripheral barred tracheides are also features in which the form which we have described diverges from Maslen's (*a*) form.

When we compare *L. oldhamius* f. *pilosus* with the type form of *L. oldhamius* (Maslen's (*β*) form) we find that the cone of the former is more fragile and the sporangia considerably smaller and shallower, while the free overlapping laminæ of the sporophylls form a more conspicuous feature. The anatomy also offers a marked contrast, since the metaxylem, instead of being massive as in *L. oldhamius*, hardly forms a continuous zone.

It should be pointed out, however, that all the characters which distinguish *L. oldhamius* f. *pilosus* from the other forms of *L. oldhamius*, including even the occurrence of hairs upon the laminæ—a unique feature as far as petrified material of *Lepidostrobus* cones are concerned—may possibly be due to the fact that the sections of this form, which we have described, are all cut near the apical region of the cone.

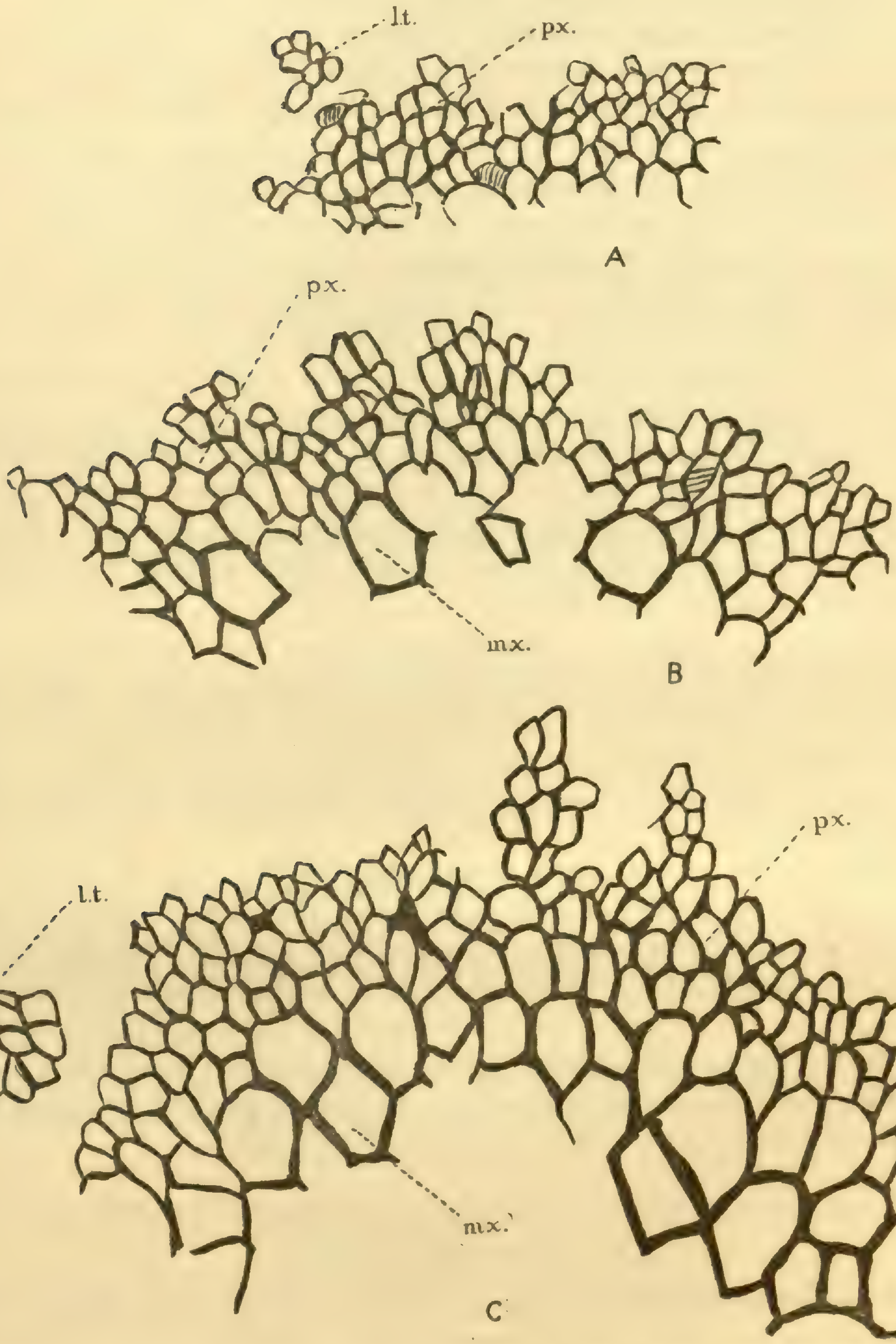
5. On a Case of Variation in the Anatomical Characters of Different Regions in a Single Cone.

In his memoir on *Lepidostrobus*, Maslen † drew attention to the need for "complete cones which can be cut up throughout their entire length so as to show what variations in structure, if any, take place in different regions in the same cone." No series of preparations, so far as I am aware, has yet been made with this object definitely in view;

* Maslen, A. J. ('99), p. 361.

† Maslen, A. J. ('99), p. 371.

Text-fig. 4.



Portions of xylem ring of *Lepidostroöus oldhamius*, Will., f. *pilosus*, from three successive sections passing through the same cone axis at different levels. (× 387.)

A. Section near cone apex; only the protoxylem is developed. *U. C. L. Coll.*, C. 16. *b*.
B. Section further from apex; metaxylem is beginning to appear. *U. C. L. Coll.*, C. 16. *b*.
C. Section still further from apex; metaxylem relatively well developed. *U. C. L. Coll.*, C. 16. *a*.

(*mx.*=metaxylem; *px.*=protoxylem; *l.t.*=sporophyll trace.)

but the two cones, which I have described in the preceding section of this paper, under the name of *L. oldhamius* f. *pilosus*, throw an interesting light on the question. There are no fewer than seven transverse sections of one of these cones (see p. 223), the two uppermost of which pass through the sporophylls above the apex of the axis. The third section (U. C. L. Coll., C. 16. *c*) traverses the tip of the axis. Here we find a vascular cylinder consisting, as seen in transverse section, of a continuous ring of protoxylem elements enclosing a pith, the metaxylem elements being completely absent (Text-fig. 4, A). In this section neither outer nor inner cortex is differentiated, and the sporophyll traces are devoid of the usual sheath of inner cortical tissue. In the next section (Watson Coll., A. 93) there is still no continuous inner cortex, but the outer cortex is differentiated, and there are a few elements of metaxylem inside the protoxylem ring. The sporophyll traces each have an inner cortical sheath, acquired at a lower level. Still further from the apex we come to a section (U. C. L. Coll., C. 16. *b*) in which the metaxylem is a little stronger (Text-fig. 4, B) and there are traces of the inner cortex, while in the next (Watson Coll., A. 94) there is more metaxylem, and the inner cortex is visible as a fragile but approximately continuous zone. The lowest section of all (U. C. L. Coll., C. 16. *a*) has the metaxylem slightly better developed (Text-fig. 4, C and Pl. 27. figs. 50 & 51), while the outer cortex has become fairly massive. It is uncertain how far distant the lowest sections were from the base of the cone, and it is possible that a more complete series would exhibit still further changes. Unfortunately the single section * of this form figured by Williamson, and the series of sections † through a cone in the Manchester University Collection resemble the series which we have just discussed in showing only the characters of the apical region of the fructification.

It is clear that, in the case of *Lepidostrobus oldhamius* f. *pilosus*, the radial width of the metaxylem and the degree of differentiation of the cortical layers varied very markedly according to the distance from the apex. This example illustrates the danger of using the anatomical features of *isolated sections* as diagnostic characters in distinguishing the species of *Lepidostrobus*. It is necessary to lay particular stress upon this point, since the attribution of these cones to the Lepidodendroid stems which bore them must depend very largely on anatomical evidence, for lack of petrified specimens showing actual continuity between the vegetative and reproductive organs.

6. On the Relation between Structure and Function in the Cone-genus *Lepidostrobus*.

The cones of *Lepidostrobus* are markedly uniform in the main features of their structure, but there is, at the same time, considerable variation both in size and form. These fructifications range from a few centimetres to about half a metre in length, and there is a degree of diversity in the form of the sporophylls recalling that to which Brongniart ‡ long ago drew attention in the modern genus *Lycopodium*.

* Gen. Coll. Brit. Mus. (Nat. Hist.), V. 8871.

† Manchester Univ. Coll., R. 385 *a* & *b*, R. 386 *a* & *b*, R. 387.

‡ Brongniart, A. ('37), p. 28 & pl. 12.

The principal modifications displayed in the cone structure of *Lepidostrobus* may be regarded as falling under two heads—first, those adaptations which appear to be primarily concerned with the protection and support of the sporangium, and, secondly, those which facilitate the nutrition of the spores.

Modifications for the protection and support of the individual sporangium were evidently rendered highly necessary by the great bulk and the delicate structure of this organ, and its "knife-edge" attachment to the sporophyll. The whole mass of sporangia must also have been greatly in need of devices to increase its rigidity. A well-developed sporophyll lamina, provided with a dorsal "heel" or flap, obviously affords very efficient protection, both to its own sporangium and to those immediately below it. This protective effect is no doubt increased by the presence of periderm, which, as we have shown in the present paper, is frequently developed towards the outer surface of the sporophyll lamina. The sporophyll pedicel is in some cases a slender stalk, triangular in section, but in other cases it is provided with lateral membranous wings. These wings support the bulging sides of the sporangium, and this support becomes even more effective when a cushion of sclerised tissue occurs on either side of the median attachment of the sporangium (*sc.c.*, Pl. 25. fig. 26 *a*). These cushions are often very well marked in cases where there is a ridge of sterile tissue forming the floor of the sporangium, and appearing, in tangential sections, as a stalk to the sporangium. In such cases the sporangium is slightly raised above the sporophyll pedicel, and hence the support given by the sclerised cushions on either side would probably become particularly valuable. Another feature, which increases the rigidity of each individual sporangium, is the radial plate of sterile tissue which so often arises from the sporangial floor (*cf.* Pl. 24. fig. 15, &c.).

The resisting power of the whole mass of sporangia is materially increased by the occurrence, in some species, of a plate-like downward keel to the sporophyll pedicel, which forms a firm barrier between the adjacent sporangia lying below it, and seems, in Williamson's words, "designed to steady the several segments of the strobilus"* (*cf.* Pl. 22. fig. 7).

The large size of the sporangia must have rendered it a matter of some difficulty to ensure an adequate supply of food and water to the developing spores. The occurrence of a ridge or pad of sterile tissue, uniting the sporangium with the sporophyll, was probably of great service in this connexion, since it increased the area of communication between archesporium and sporophyll (*cf.* Pl. 25. figs. 26 & 26 *a*). This ridge, in one of the species described in the present paper, contained numerous transfusion tracheides, by means of which water could be conveyed from the sporophyll trace to the developing spores (Pl. 25. fig. 27). A still further modification of the floor of the sporangium consists in the development of sterile trabeculæ, or a median sterile plate, penetrating for a considerable distance into the cavity. Such a structure, as Bower † has pointed out in the case of *L. Brownii*, no doubt facilitated the nutrition of the spores. In *L. Brownii*, moreover, as Zeiller ‡ has recently shown, transfusion tracheides occur on the upper side

* Williamson, W. C. ('73), p. 295.

† Bower, F. O. ('94), p. 528.

‡ Zeiller, R. ('11), p. 32.

of the vascular bundle throughout the sporophyll pedicel. By their means, water could easily pass from the sporophyll trace to the trabeculæ. In *Lepidostrobus oldhamius* the sterile plates are best developed in the young sporangia whose spores have not completed their development, and in which the need for the conduction of food and water must be at its maximum (see Pl. 24. fig. 15).

In all the cases in *Lepidostrobus* in which transfusion tracheides occur in the sporophyll, these elements are noticeably abundant at the junction of limb and pedicel. Here they are chiefly massed on the ventral side of the sporophyll trace, in the neighbourhood of the ligule (*cf.* Pl. 26. figs. 41, 43, 44, 45). Among living plants we find an analogy for this development of transfusion tissue in the tracheidal cup which surrounds the base of the ligule in *Selaginella lævigata*, Baker, var. *Lyallii*, Spring.* Harvey Gibson has suggested† that the ligule in *Selaginella* is a mucilage organ, whose function is the temporary one of keeping the growing point and young leaves moist. It seems quite possible that it played the same part in the cones of *Lepidostrobus*, and that, in both cases, the performance of this function is facilitated by the tracheides which occur in this region of the leaf. The idea that the office of the ligule may merely be to keep the delicate organs of the developing cone from desiccation, and that it is functionless when the fructification is mature, gains some confirmation from Zeiller's‡ discovery that, in *L. Brownii*, this organ is quite ephemeral, and only survives in the young apical region of the petrified cone.

7. List of Memoirs cited.

Arber, A. ('13).—"On the Structure of *Lepidostrobus laminatus*, sp. nov." Rep. Brit. Assoc. Dundee, (1912) p. 674, 1913.

Arber, E. A. N. ('12).—"On the Fossil Flora of the Forest of Dean Coalfield (Gloucestershire), and the Relationships of the Coalfields of the West of England and South Wales." Phil. Trans. Roy. Soc. London, Ser. B, vol. 202. (1912) p. 233.

Binney, E. W. ('71).—Observations on the Structure of Fossil Plants found in the Carboniferous Strata. Part II. *Lepidostrobus* and some Allied Cones. Palæontographical Society, London, 1871.

Bower, F. O. ('93).—"On the Structure of the Axis of *Lepidostrobus Brownii*, Schpr." Ann. Bot. vol. vii. (1893) p. 329.

Bower, F. O. ('94).—"Studies in the Morphology of Spore-producing Members.—Equisetineæ and Lycopodineæ." Phil. Trans. Roy. Soc. London, Ser. B, vol. 185. Pt. 1. (1894) p. 473.

Bower, F. O. ('08).—The Origin of a Land Flora. London, 1908.

Brongniart, A. ('37).—Histoire des Végétaux Fossiles. Vol. ii., 1837–38.

Brown, R. ('48).—"Some Account of an undescribed Fossil Fruit." Ann. & Mag. Nat. Hist. 2nd ser. vol. i. (1848) p. 376.

Brown, R. ('51).—"Some Account of an undescribed Fossil Fruit." Trans. Linn. Soc. London, vol. xx. (1851) p. 469.

Coulter, J. M., & W. J. G. Land ('11).—"An American *Lepidostrobus*." Bot. Gaz. vol. li. (1911) p. 449.

---

* Gibson, R. J. H. ('96), pl. 8. fig. 21.

† Gibson, R. J. H. ('96), p. 87.

‡ Zeiller, R. ('11), pp. 33 & 34.

Gibson, R. J. H. ('96). "Contributions towards a Knowledge of the Anatomy of the genus *Selaginella*, Spr[ing]. Pt. II. The Ligule." Ann. Bot. vol. x. (1896) p. 77.

Hooker, J. D. ('48).—"Remarks on the Structure and Affinities of some *Lepidostrobi*." Mem. Geol. Survey Gt. Brit. vol. ii. pt. ii. p. 440, 1848.

Kidston, R. ('83).—"Report on Fossil Plants, collected by the Geological Survey of Scotland in Eskdale and Liddesdale." Trans. Roy. Soc. Edinb. vol. xxx. (1883) p. 531.

Maslen, A. J. ('98).—"The Ligule in *Lepidostrobus*." Ann. Bot. vol. xii. (1898) p. 256.

Maslen, A. J. ('99).—"The Structure of *Lepidostrobus*." Trans. Linn. Soc. London, 2nd Ser. Bot. vol. v. (1899) p. 357.

Scott, D. H. ('00).—Studies in Fossil Botany. Ed. I. London, 1900.

Scott, R. (Mrs. D. H. Scott) ('06).—"On the Megaspore of *Lepidostrobus foliaceus*." New Phyt. vol. v. (1906) p. 116.

Seward, A. C. ('10).—Fossil Plants. Vol. ii., Cambridge, 1910.

Watson, D. M. S. ('09).—"On *Mesostrobus*, a New Genus of Lycopodiaceous Cones from the Lower Coal Measures, with a Note on the Systematic Position of *Spencerites*." Ann. Bot. vol. xxiii. (1909) p. 379.

Williamson, W. C. ('73).—"On the Organization of the Fossil Plants of the Coal-Measures. Part III. Lycopodiaceæ (*continued*)." Phil. Trans. Roy. Soc. London, vol. 162, Pt. II. (1873) p. 283 (for 1872).

Williamson, W. C. ('94).—"On the Organization of the Fossil Plants of the Coal-Measures. Part XIX." Phil. Trans. Roy. Soc. London, Ser. B, vol. 184, 1894 (for 1893) p. 1.

Zalessky, M. ('08).—"Végétaux fossiles du terrain carbonifère du Bassin du Donetz. II. Étude sur la structure anatomique d'un *Lepidostrobus*." Mém. Comité Géol. St. Pétersb., N. S. Livr. 46, 1908.

Zeiller, R. ('11).—"Étude sur le *Lepidostrobus Brownii* (Unger) Schimper." Mém. de l'Acad. des Sci. Paris, t. 52, 1911.

EXPLANATION OF THE PLATES.

Plates **21**, **22**, **23**, **27** are from Photographs by W. Tams, Cambridge.
Plates **24**, **25**, **26** are from Drawings by the author.

Plate 21.

Lepidostrobus oldhamius, Will. Figs. 1–3.

Fig. 1. General view of an oblique section through the apex of a cone to show plates of sterile tissue arising from the floors of the sporangia, (*st.p.*). *Sedgwick Mus. Coll.*, Slide 281 (before grinding down). ($\times 7\frac{1}{2}$ circa.) The sporangium marked * is shown on a larger scale in fig. 2, and the sterile plate † in Pl **24**. fig. 16.

(*ap.*=cone apex; *sp.*=spores; *l.*=sporophyll; *lg.*=ligule.)

Fig. 2. Enlargement of the sporophyll and sporangium, marked * in fig. 1, to show ligule. *Sedgwick Mus. Coll.*, Slide 281. ($\times 21$ circa.)

(*spm.w.* = sporangium wall; *sp.* = spores; *s.a.p.*=sub-archesporial pad; *l.*=sporophyll; *l.t.*=vascular bundle of sporophyll; *lg.*=ligule.)

Fig. 3. General view of the same oblique section reproduced in fig. 1 after it had been further ground down to render it more transparent. *Sedgwick Mus. Coll.*, Slide 281. (×7½ circa.) The sporophyll and ligule shown in fig. 2 were destroyed in the grinding.

(*ap.*=apex of cone; *l.*=sporophyll; *sp.*=spores; *spm.w.*=sporangium wall; *s.a.p.*=sub-archesporial pad; *st.p.*=plate of sterile tissue arising from the floor of the sporangium.)

LEPIDOSTROBUS BINNEYANUS, sp. nov. Fig. 4.

Fig. 4. Transverse section of central part of cone axis. *Binney Coll.*, Q. *a*. 1. (×45 circa.) The sporophyll trace marked *l.t.** is shown on a larger scale in Pl. 24. fig. 23, and that marked *l.t.*† in Pl. 24. fig. 22.

(*v.c.*= vascular cylinder; *p.* = pith; *mx.* = metaxylem; *px.* = protoxylem; *i.c.* = inner cortex; *i.c.s.*=inner cortical sheath surrounding the sporophyll trace; *l.t.*=sporophyll trace.)

PLATE 22.

LEPIDOSTROBUS BINNEYANUS, sp. nov. Figs. 5–8.

Fig. 5. Radial longitudinal section through vascular cylinder of cone axis. *Binney Coll.*, Q. *a*. 6. (×105 circa.)

(*mx.*=metaxylem; *px.*=protoxylem; *p.*=pith.)

Fig. 6. Part of a transverse section of a cone passing through two sporophylls near the base of their upturned lobes and through sporangia. *Binney Coll.*, Q. *β*. 2. (×35 circa.) The cellular outgrowth marked *l.o.** is shown on a larger scale in Pl. 25. fig. 30.

(*l.* = sporophyll; *l.t.* = vascular bundle of sporophyll; *spm.w.* = sporangium wall; *sp.*=spores; *pd.*=periderm; *l.o.*=cellular outgrowth from sporophyll.)

Fig. 7. Two sporophylls seen in tangential section. *Binney Coll.*, Q. *a*. 4. (×47 circa.)

(*p.w.*=wing of pedicel; *sc.c.*=lateral sclerised cushion of pedicel; *st.r.*=median ridge of tissue by which the sporangium is attached; *k.p.*=keel of pedicel; *ep.* = epidermis; *hy.*=hypoderma; *l.t.*=vascular bundle of pedicel; *spm.w.*=sporangium wall.)

Fig. 8. Tangential section of the keel of another sporophyll from the same preparation as fig. 7, in which the conducting tissue is better shown. *Binney Coll.*, Q. *a*. 4. (×47 circa.)

(*k.p.*=keel of pedicel; *sc.c.*=lateral sclerised cushion of pedicel; *x.*=xylem; *t.t.*=transfusion tracheides; *ep.*=epidermis; *hy.*=hypoderma.)

LEPIDOSTROBUS GRACILIS, sp. nov. Fig. 9.

Fig. 9. A single sporophyll, cut almost radially, incomplete at the proximal end. *Sedgwick Mus. Coll.*, Slide 276. (×14 circa.)

(*l.*=sporophyll lamina; *sc.t.*=dorsal sclerised tissue of sporophyll; *l.h.*=heel of sporophyll; *l.p.*=pedicel of sporophyll.)

PLATE 23.

LEPIDOSTROBUS GRACILIS, sp. nov. Figs. 10–12.

Fig. 10. General view of a longitudinal section through a cone, which is tangential in the middle and approximately radial at the sides. *Sedgwick Mus. Coll.*, Slide 276. (×12 circa.)

(*l.*=sporophyll; *l.h.*=heel of sporophyll; *l.t.*=sporophyll trace; *k.p.*=keel of pedicel; *p.w.* = wing of pedicel; *sc.c.* = lateral sclerised cushion of pedicel; *spm.w.* = sporangium wall.)

Fig. 11. Transverse section of cone axis. *Sedgwick Mus. Coll.*, Slide 278. (×47 circa.)
(*p.*=pith; *mx.*=metaxylem; *px.*=protoxylem; *l.t.*=sporophyll trace; *i.c.*=inner cortex; *o.c.*=outer cortex; *l.p.b.*=base of sporophyll pedicel.)

Fig. 12. Central part of the axis shown in fig. 11, enlarged. *Sedgwick Mus. Coll.*, Slide 278. (×140 circa.)
(*p.* = pith; *mx.* = metaxylem; *px.* = protoxylem; *l.t.* = sporophyll trace; *i.c.* = inner cortex.)

LEPIDOSTROBUS OLDHAMIUS, Will., f. MINOR. Figs. 13, 14.

Fig. 13. General view of a section, which is radial as regards most of the sporophylls, but tangential as regards the axis. *Binney Coll.*, AM. 27. (×4½ circa.)
(*l.*=sporophyll; *l.p.*=pedicel of sporophyll; *sp.*=spores; *l.t.*=sporophyll trace.)

Fig. 14. Apical portion of another section of the same cone as that seen in fig. 13, showing a number of sporophylls and sporangia in tangential section. *Binney Coll.*, AM. 26. (×4½ circa.)
(*l.*=sporophyil; *l.p.*=sporophyll pedicel; *spm.*=sporangium.)

PLATE 24.

LEPIDOSTROBUS OLDHAMIUS, Will. Figs. 15–17.

Fig. 15. General view of part of the cone photographed in Pl. 21. fig. 1. *Sedgwick Mus. Coll.*, Slide 281. (×14.) The sporangium which is marked * is that indicated by an asterisk in Pl. 21. fig. 1.
(*l.*=sporophyll; *l.t.*=vascular bundle of sporophyll; *par.*=parichnos space; *lg.*=ligule; *spm.w.* = sporangium wall; *sp.* = spores; *s.a.p.* = sub-archesporial pad; *st.p.* = plate of sterile tissue arising from the floor of the sporangium.)

Fig. 16. Enlarged drawing of the sterile plate from the sporangium marked † in Pl. 21. fig. 1. *Sedgwick Mus. Coll.*, Slide 281. (× 77 circa.)

Fig. 17. Sporophyll pedicel and base of sporangium in tangential section to show the sterile plate (*st.p.*) in a sporangium older than that shown in fig. 16. *U. C. L. Coll.*, C. 19. (× 23.)
(*s.a.p.*=sub-archesporial pad; *spm.w.*=sporangium wall; *l.p.*=sporophyll pedicel.)

LEPIDOSTROBUS BINNEYANUS, sp. nov. Figs. 18–25.

Fig. 18. Metaxylem tracheides from the radial section of the cone axis photographed in Pl. 22. fig. 5, to show the vertical striations connecting the scalariform thickenings. *Binney Coll.*, Q. *a.* 6. (× 318.)

Fig. 19. Sculpturing of a spiral protoxylem tracheid seen in longitudinal section, from the same preparation as fig. 18. *Binney Coll.*, Q. *a.* 6. (× 318.)

Fig. 20. Radial longitudinal section, not quite median, passing through the distal end of a sporophyll pedicel and showing the distal attachment of the sporangium. *Binney Coll.*, Q. *β.* 4. (× 47.)
(*l.* = sporophyll lamina; *l.h.* = heel of sporophyll lamina; *l.p.* = sporophyll pedicel; *t.t.* = transfusion tracheides; *spm.w.* = sporangium wall; *sp.* = spores; *lg.* = ? ligule; *pd.* = periderm.)

Fig. 21. Radial longitudinal section through the proximal end of a sporophyll pedicel, showing the proximal attachment of the sporangium and the oblique downwardly directed course of the sporophyll trace in the axis. *Binney Coll.*, Q. *a.* 6. (× 47.)
(*ax.*=cone axis; *l.t.*=vascular bundle destined for sporophyll; *lp.*=sporophyll pedicel; *spm.w.*=sporangium wall; *st.r.*=ridge of sterile tissue rising into base of sporangium; *sp.*=spores.)

Fig. 22. The xylem of a sporophyll trace in transverse section shortly after it has left the central cylinder. The same bundle is marked *l.t.*† in the photograph reproduced in Pl. **21**. fig. 4. *Binney Coll.*, Q. *a*. 1. (× 318.)

(In this figure and in fig. 23 the lower side of the trace faces the centre of the axis.)

Fig. 23. A sporophyll trace in transverse section, passing through the sclerised inner cortex. The same bundle is marked *l.t.** in the photograph reproduced in Pl. **21**. fig. 4. *Binney Coll.*, Q. *a*. 1. (× 318.)

(*xy.*=xylem; *i.c.*=inner cortex; *i.c.s.*=inner cortical sheath enclosing sporophyll trace.)

Fig. 24. Tetrad of spores. *Binney Coll.*, Q. *a*. 1. (× 318.)

Fig. 25. Mature spores showing the triradiate marking and equatorial border. *Binney Coll.*, Q. *β*. 4. (× 318.)

Plate 25.

Lepidostrobus Binneyanus, sp. nov. (*continued*). Figs. 26–30.

Fig. 26. Tangential section of a sporophyll and sporangium somewhat crushed and distorted. *Binney Coll.*, Q. *a*. 4. (× 23.)

(*p.w.*=wing of pedicel; *k.p.*=keel of pedicel; *sc.c.*=sclerised cushion; *l.t.*=sporophyll trace; *spm.w.*=sporangium wall; *st.r.*=ridge of sterile tissue forming floor of sporangium.)

Fig. 26 *a*. Part of the sporophyll and sporangium shown in fig. 26, more highly magnified. *Binney Coll.*, Q. *a*. 4. (× 47.)

(*p.w.*=wing of pedicel; *k.p.*=keel of pedicel; *sc.c.*=sclerised cushion; *l.t.*=sporophyll trace; *t.t.*=transfusion tracheides; *ep.*=epidermis; *hy.*=hypoderma; *spm.w.*=sporangium wall; *st.r.*=ridge of sterile tissue forming floor of sporangium.)

Fig. 27. A small part of a tangential section passing through a sporophyll pedicel, similar to that shown in fig. 26 *a*. The sterile ridge (*st.r.*) in this case contains numerous transfusion tracheides (*t.t.*), and there is apparently a median plate of sterile tissue (*st.p.*) arising from the sterile ridge. *Binney Coll.*, Q. *a*. 3. (× 77.)

(*spm.w.*=continuation of sporangium wall down the side of the sterile ridge; *sc.c.*= sclerised cushion of sporophyll pedicel.)

Fig. 28. Xylem elements and some transfusion tracheides from a tangential section of a sporophyll similar to that shown in figs. 26 and 26 *a*. *Binney Coll.*, Q. *a*. 4. (× 318.)

(*xy.*=xylem; *t.t.*=transfusion tracheides.)

Fig. 29. Part of the dorsal surface of one of the transverse sections of sporophyll laminæ photographed in Pl. **22**. fig. 6, to show radial arrangement of cells indicating periderm formation (*pd.*). *Binney Coll.*, Q. *β*. 2. (× 318.)

Fig. 30. Cellular outgrowth from the ventral surface of a sporophyll lamina. This outgrowth is seen on a smaller scale, marked *l.o.**, in the transverse section photographed in Pl. **22**. fig. 6. *Binney Coll.*, Q. *β*. 2. (× 318.)

Lepidostrobus gracilis, sp. nov. Figs. 31–39.

Fig. 31. Obliquely tangential section through three sporophyll bases. The two lower sporophylls (*b* and *c*) are still connected by tissue belonging to the outer cortex, but the upper one (*a*) has become free from the cone axis. *Sedgwick Mus. Coll.*, Slide 280. (× 14.)

(*l.p.b.*=base of sporophyll pedicel; *xy.*=xylem; *ph.*=so-called phloem; *par.*=parichnos space.)

Fig. 32. Tangential section through a sporophyll pedicel, a little further from the axis than *a* in fig. 31, but not so far out as to show the attachment of the sporangium. *Sedgwick Mus. Coll.*, Slide 280. (× 14.)

(*spm.w.*=sporangium wall; *xy.*=xylem; *ph.*=so-called phloem; *par.*=parichnos space.)

Fig. 33. Tangential section through a sporophyll pedicel further from the axis than fig. 32. The attachment of the base of the sporangium is shown. The sporangium has dehisced and the walls are displaced. *Sedgwick Mus. Coll.*, Slide 276. (× 14.)

(*pw.*=wing of pedicel; *sc.c.*=sclerised cushion; *k.p.*=keel of pedicel; *l.t.*=vascular bundle of sporophyll; *spm.w.*=sporangium wall; *st.r.*=ridge of sterile tissue forming floor of sporangium; *st.p.*=sterile upgrowth from floor of sporangium.)

Fig. 34. Vascular bundle from the sporophyll base marked *l.p.b.*(*c*) in fig. 31. *Sedgwick Mus. Coll.*, Slide 280. (× 318.)

(*xy.*=xylem; *ph.*=so-called phloem.)

Fig. 35. Obliquely transverse section through the vascular bundle of a sporophyll near the distal end of the pedicel, showing xylem (*xy.*) flanked by transfusion tracheides (*t.t.*). *Sedgwick Mus. Coll.*, Slide 279. (× 318.)

Fig. 36. Part of a transverse section of a sporophyll lamina to show traces of periderm formation near the dorsal surface. *Sedgwick Mus. Coll.*, Slide 278. (× 318.)

(*pd.*=periderm; *ep.?*=layer which may represent remains of epidermis.)

Fig. 37 *a* & *b*. Transverse sections through the columnar layer of the wall of the sporangium shown in fig. 32. The upper side represents the inner surface. *Sedgwick Mus. Coll.*, Slide 280. (× 318.)

Fig. 37 *a* represents a part of the wall close to the dehiscence line, while fig. 37 *b* represents part of the thicker region of the wall which is adjacent to the sporophyll pedicel.

Fig. 38. Tangential section through the columnar layer of the sporangium wall. *Sedgwick Mus. Coll.*, Slide 279. (× 318.)

Fig. 39. Spores. *Sedgwick Mus. Coll.*, Slide 279. (× 318.)

Plate 26.

Lepidostrobus gracilis, sp. nov. (*continued*). Figs. 40–42.

Fig. 40. Tangential section passing through a sporophyll and the base of a sporangium. *Sedgwick Mus. Coll.*, Slide 279. (× 193.)

(*k.p.*=keel of pedicel; *p.w.*=wing of pedicel; *sc.c.*=lateral sclerised cushion of pedicel; *xy.*=xylem; *ph.*=so-called phloem; *spm.w.*=sporangium wall; *st.r.*=ridge of sterile tissue occupying base of sporangium.)

Fig. 41. Sporophyll from transverse section of a cone to show the ligule (*lg.*) in the ligular pit (*lg.p.*). The sporophyll pedicel is torn. *Sedgwick Mus. Coll.*, Slide 278. (× 14.)

(*l.*=lamina of sporophyll; *xy.*=xylem; *t.t.*=transfusion tracheides.)

Fig. 42. Transverse section of the sporophyll trace near the base of the lamina. The tissue surrounding the bundle is broken, and probably some transfusion tissue is lost on the right-hand side. *Sedgwick Mus. Coll.*, Slide 279. (× 318.)

(*xy.*=xylem; *t.t.*=transfusion tracheides.)

Lepidostrobus oldhamius, Will., f. minor. Figs. 43–49.

Fig. 43. Radial longitudinal sections of two sporophylls. *Binney Coll.*, AM. 27. (× 14.)

(*ax.*=axis; *l.p.*=sporophyll pedicel; *l.*=sporophyll lamina; *l.h.*=heel of sporophyll lamina; *lg.p.*=ligular pit; *par.*=parichnos; *spm.w.*=sporangium wall; *sp.*=spores; *xy.*=xylem; *t.t.*=transfusion tracheides. The region marked with an asterisk is reproduced on a larger scale in fig. 44.)

Fig. 44. High-power drawing of xylem (*xy.*) and transfusion tracheides (*t.t.*) from the region marked with an asterisk in the base of the upturned lamina of the lower sporophyll shown in fig. 43. *Binney Coll.*, AM. 27. (× 318.)

Fig. 45. Tangential section passing through a sporophyll and showing what appears to be the ligule (?*lg.*). *Binney Coll.*, AM. 27. (× 14.)

(*xy.*=xylem ; *t.t.*=transfusion tracheides.)

Fig. 46. Tangential section passing through a sporophyll pedicel and sporangium. *Binney Coll.*, AM. 29. (× 14.)

(*spm.w.*=sporangium wall ; *sc.c.*=lateral sclerised cushion ; *st.p.*=plate of sterile tissue arising from the sporangium floor.)

Fig. 47. Tangential section passing through a sporophyll pedicel bearing an immature or abortive sporangium. *Binney Coll.*, AM. 28. (× 193.)

(*p.w.*=wing of pedicel ; *sc.c.*=sclerised cushion of pedicel ; *xy.*=xylem ; *spm.w.*=sporangium wall.)

Fig. 48. Obliquely tangential section of a sporangium wall, passing through outer columnar layer (*o.l.*) and inner thin-walled layer (*i.l.*). *Binney Coll.*, AM. 26. (× 318.)

Fig. 49. Spores. *Binney Coll.*, AM. 26. (× 318.)

Plate 27.

Lepidostrobus oldhamius, Will., f. pilosus. Figs. 50–54.

Fig. 50. Transverse section through the cone at some distance from the apex. *U. C. L. Coll.*, C. 16.*a*. (× 6.)

(*v.c.*=central cylinder of cone axis ; *o.c.*=outer cortex of cone axis ; *p.w.*=wing of sporophyll pedicel ; *spm.w.*=sporangium wall ; *sp.*=spores ; *lg.*=ligule ; *l.*=upturned lamina of sporophyll.)

Fig. 51. Central part of the section shown in fig. 50 more highly magnified. *U. C. L. Coll.*, C. 16.*a*. (× 61.)

(*v.c.*=central cylinder of cone axis ; *m.*=space from which the pith has disappeared ; *mx.*=metaxylem ; *px.*=protoxylem ; *l.t.*=sporophyll trace ; *i.c.*=inner cortex.)

Fig. 52. Transverse section through the apex of the same cone as that from which the sections represented in figs. 50 and 51 were taken, passing through the sporophylls above the top of the axis. Towards the outside the sporophylls are cut through near their apices, and are more triangular in section and more sclerised than those further in, which are cut nearer the base of the upturned lobe. *Watson Coll.*, A. 92. (× 6.)

Fig. 53. Central part of the section photographed in fig. 52, more highly magnified to show the tangled hairs (*h.*). *Watson Coll.*, A. 92. (× 77 circa.)

(*l.*=lamina of sporophyll.)

Fig. 54. Transverse section through another cone, so near the apex of the cone axis that the outer and inner cortex and the metaxylem are scarcely differentiated. *Manchester University Coll.*, R. 386. *b*. (× 6.)

(*v.c* =vascular cylinder ; *l.*=upturned limb of sporophyll ; *spm.w.*=sporangium wall ; *lg.*=one of the six ligules which occur in this section.)

Lepidostrobus oldhamius, Will. Figs. 55 & 56.

Fig. 55. Tangential section of sporophyll and sporangium from an obliquely transverse section of a cone to show the plate of sterile tissue (*st.p.*) rising into the cavity of the sporangium. *Scott Coll.*, 2456. (× 12 circa.)

(*l.t.*=sporophyll trace ; *l.p.*=sporophyll pedicel ; *spm.w.*=sporangium wall ; *sp.*=spores.)

Fig. 56. Transverse section of the outer edge of the upturned limb of a sporophyll to show periderm (*pd.*). *Scott Coll.*, 1200. (× 82.)

1.

4.

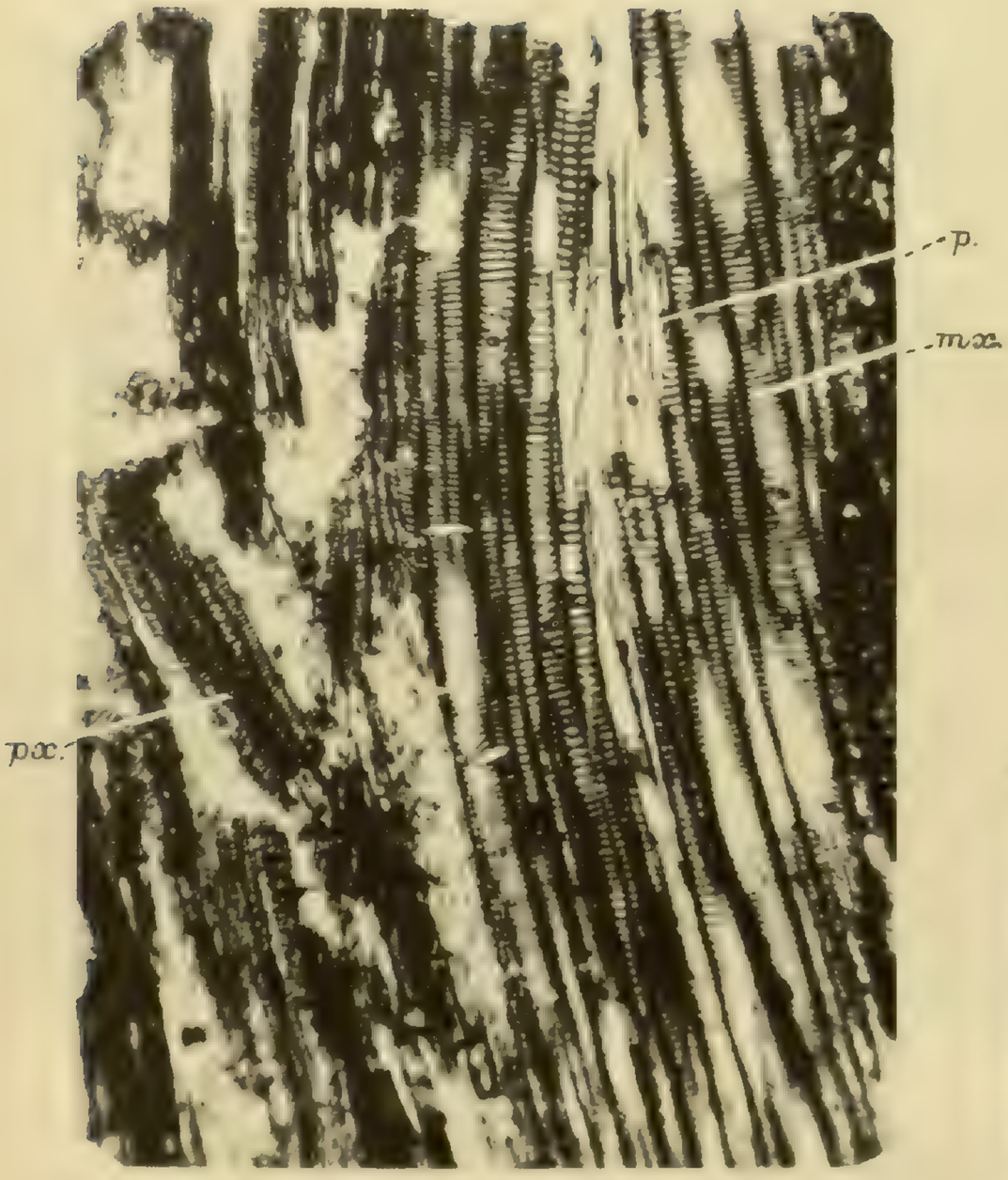
2.

3.

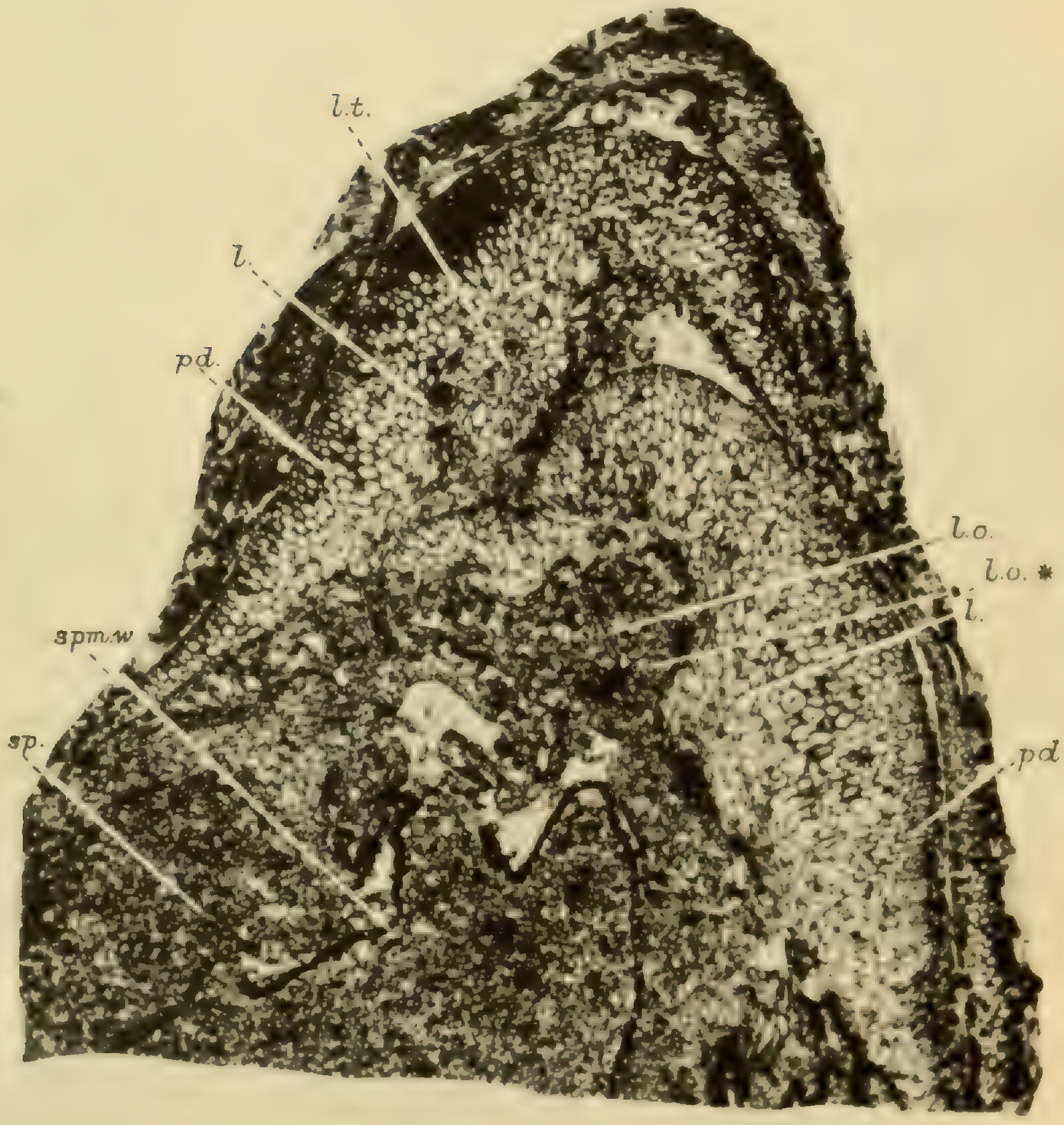
W. Tame photo

Huth coll

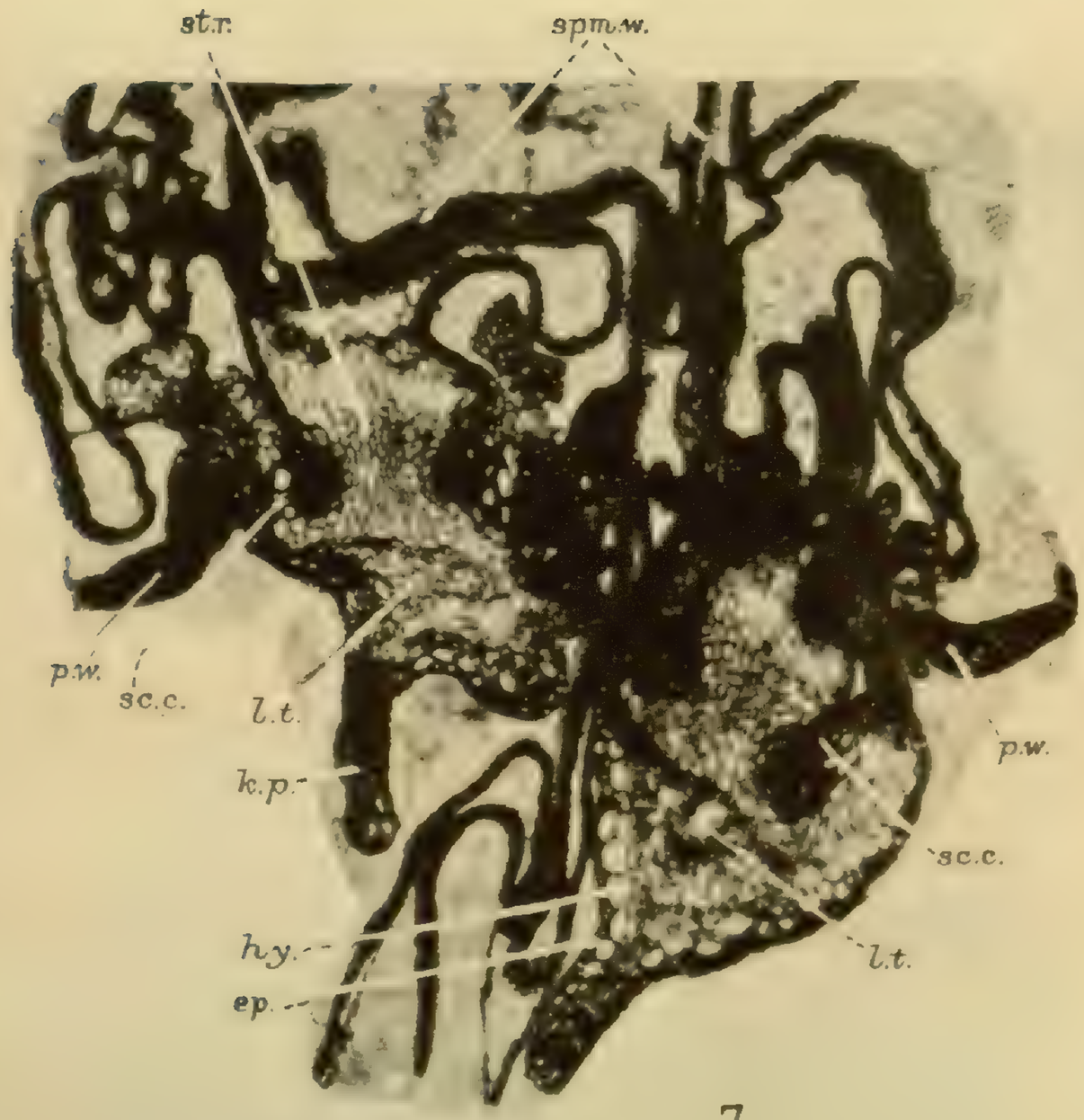
LEPIDOSTROBUS OLDHAMIUS Will. Figs 1-3, L. BINNEYANUS Fig. 4.



5.

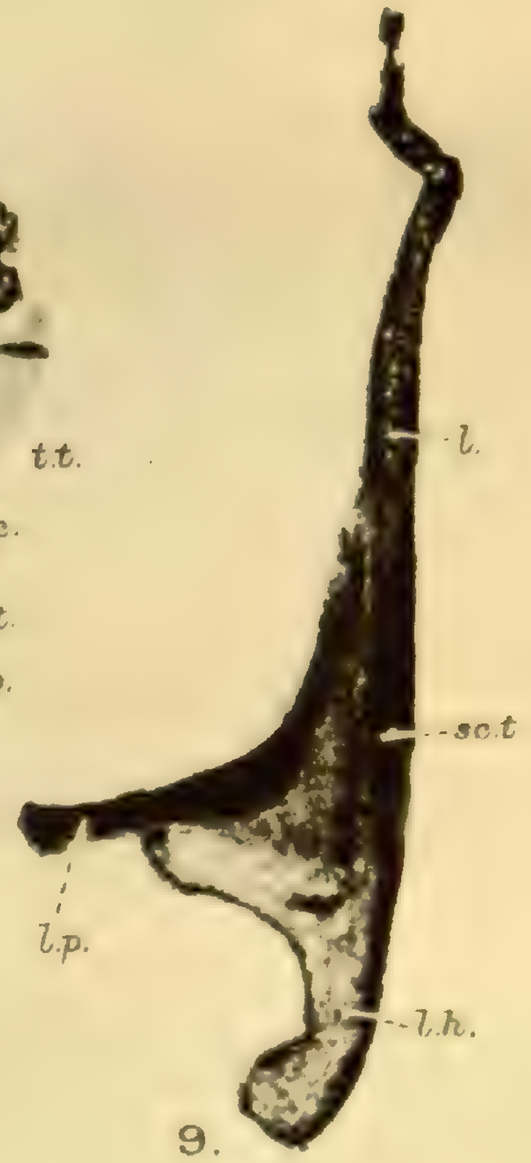


6.



7.

8.

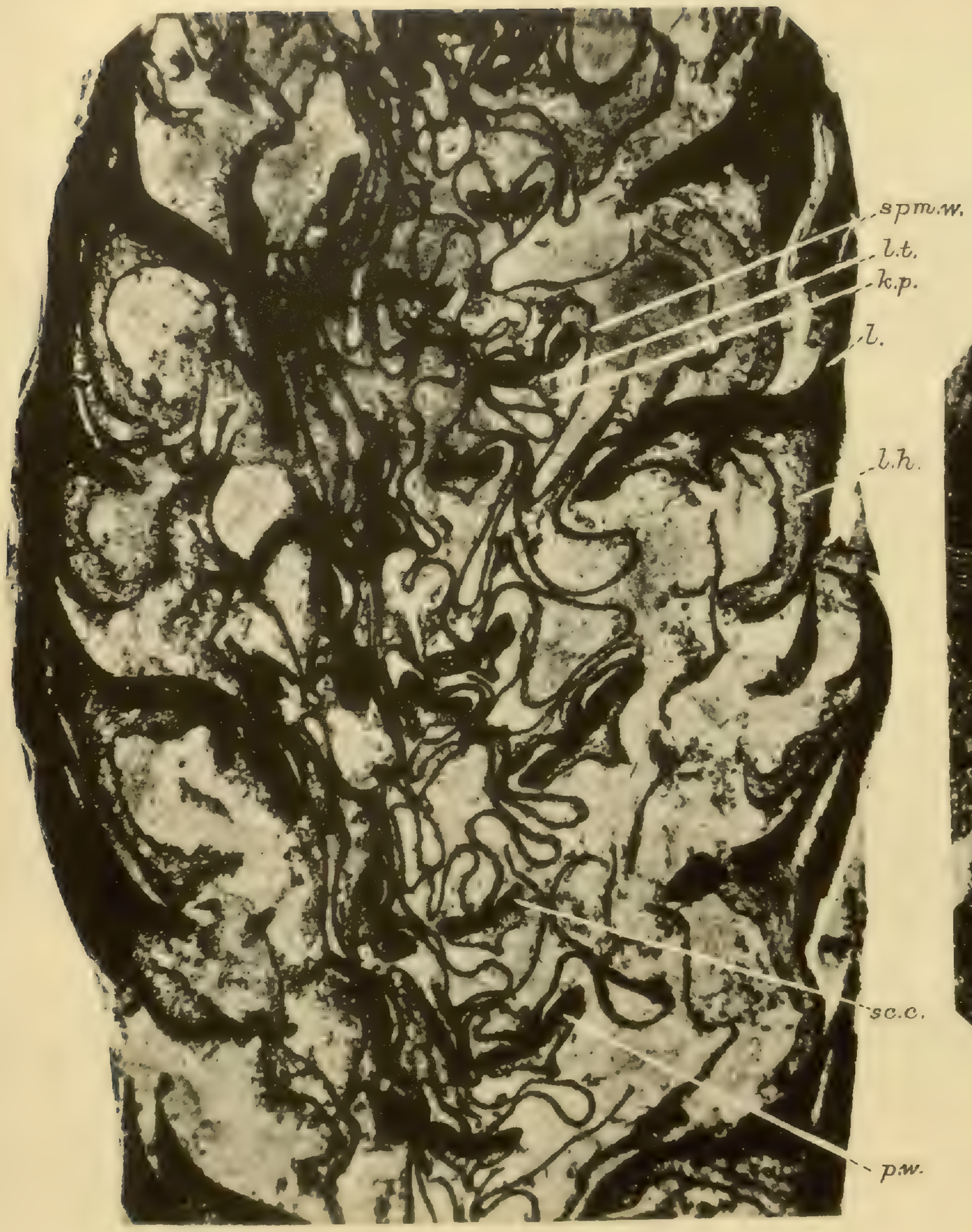


9.

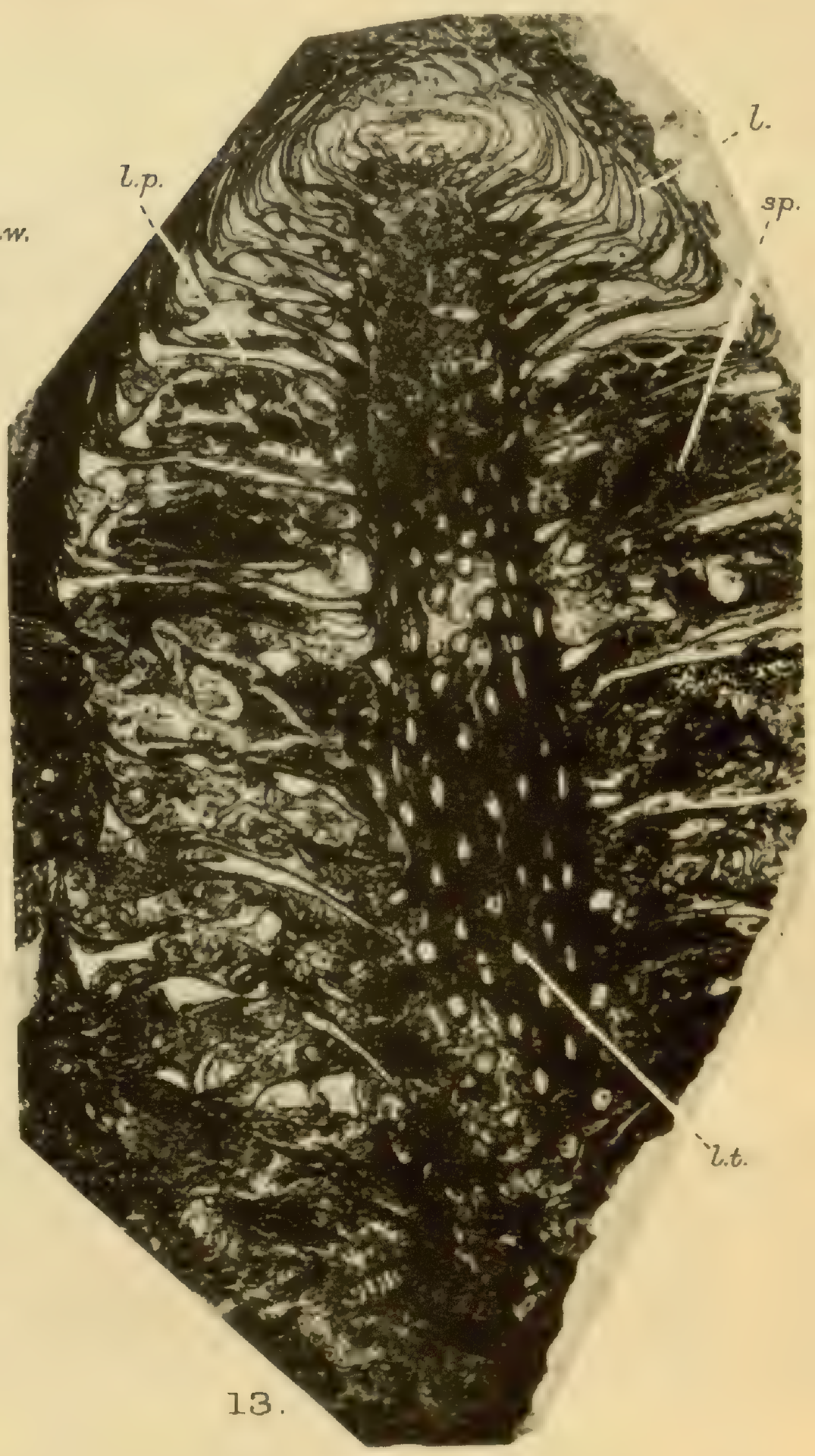
W. Tams phot.

Huth coll

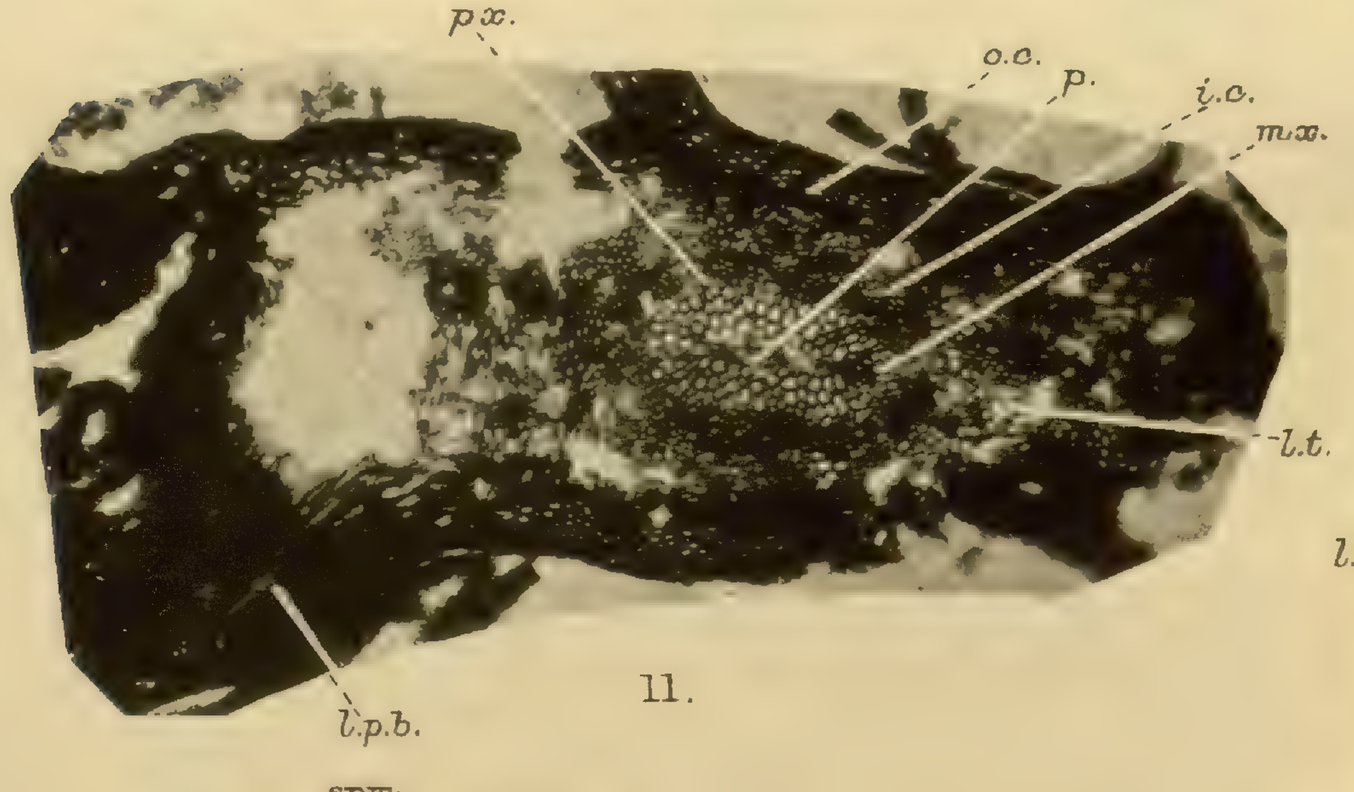
LEPIDOSTROBUS BINNEYANUS sp. nova. Figs. 5–8, L. GRACILIS sp. nova. Fig. 9.



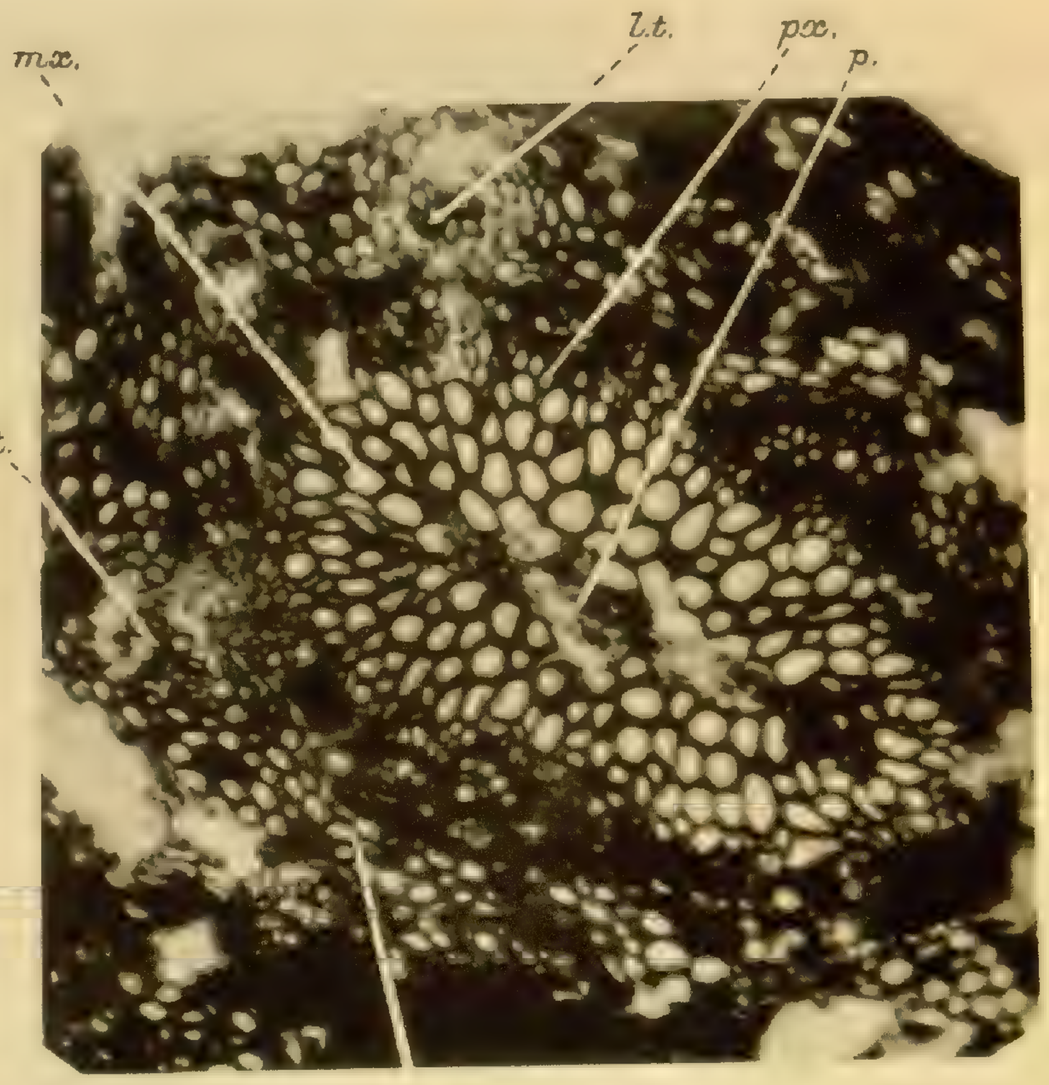
10.



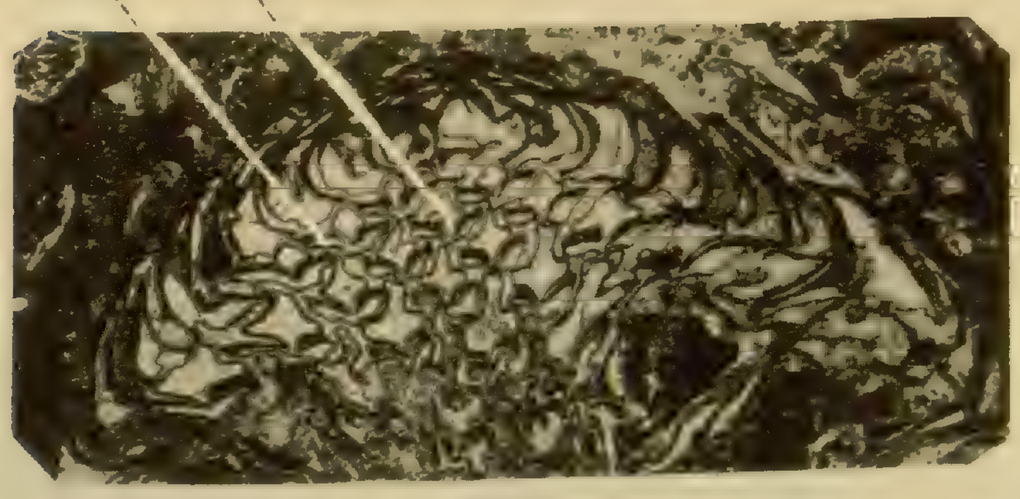
13.



11.



12.



14.

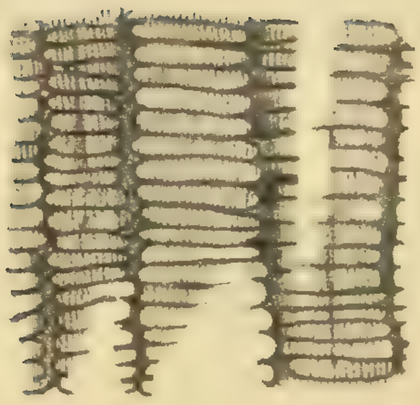
W. Tams phot. Huth coll.

LEPIDOSTROBUS GRACILIS sp. nova. Figs 10–12, L. OLDHAMIUS Will. f. minor Figs 13, 14.

15.

16.

17.



18.

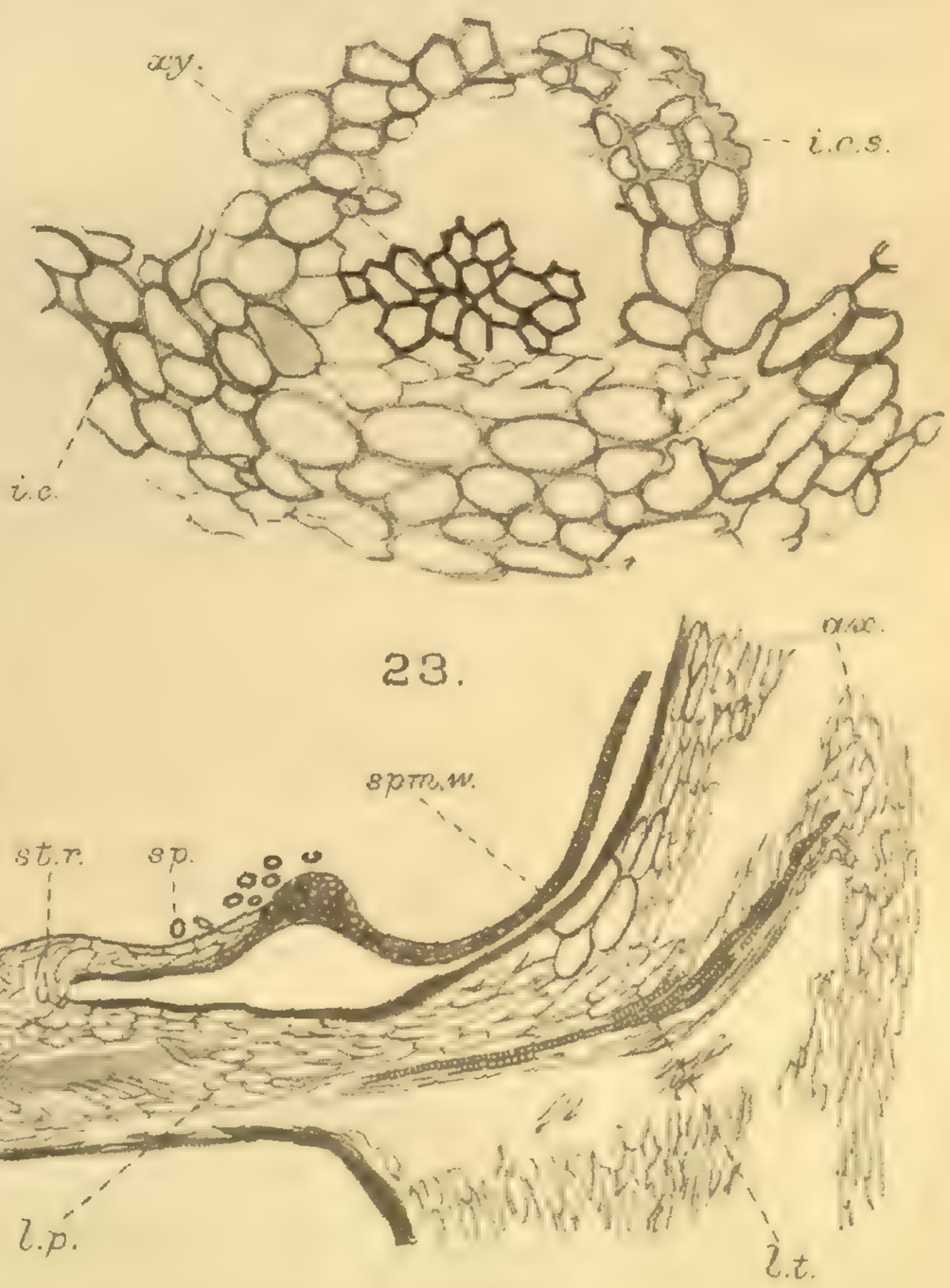
22.

24.

25.

19.

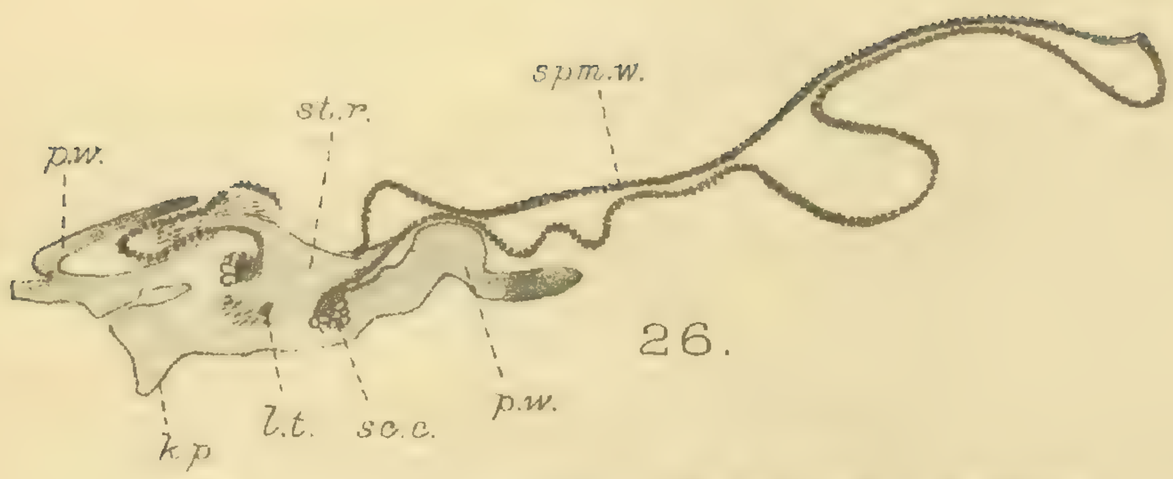
20.



23.

21.

LEPIDOSTROBUS OLDHAMIUS Figs 15-17, L. BINNEYANUS Figs 18-25.



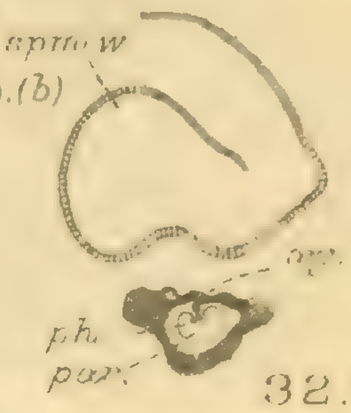
26.

26a.

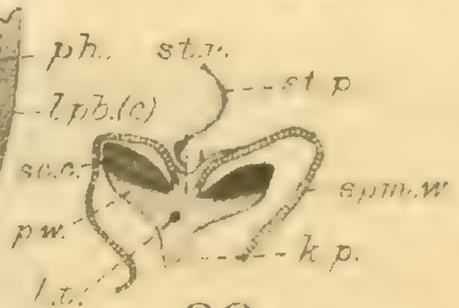
29.

30.

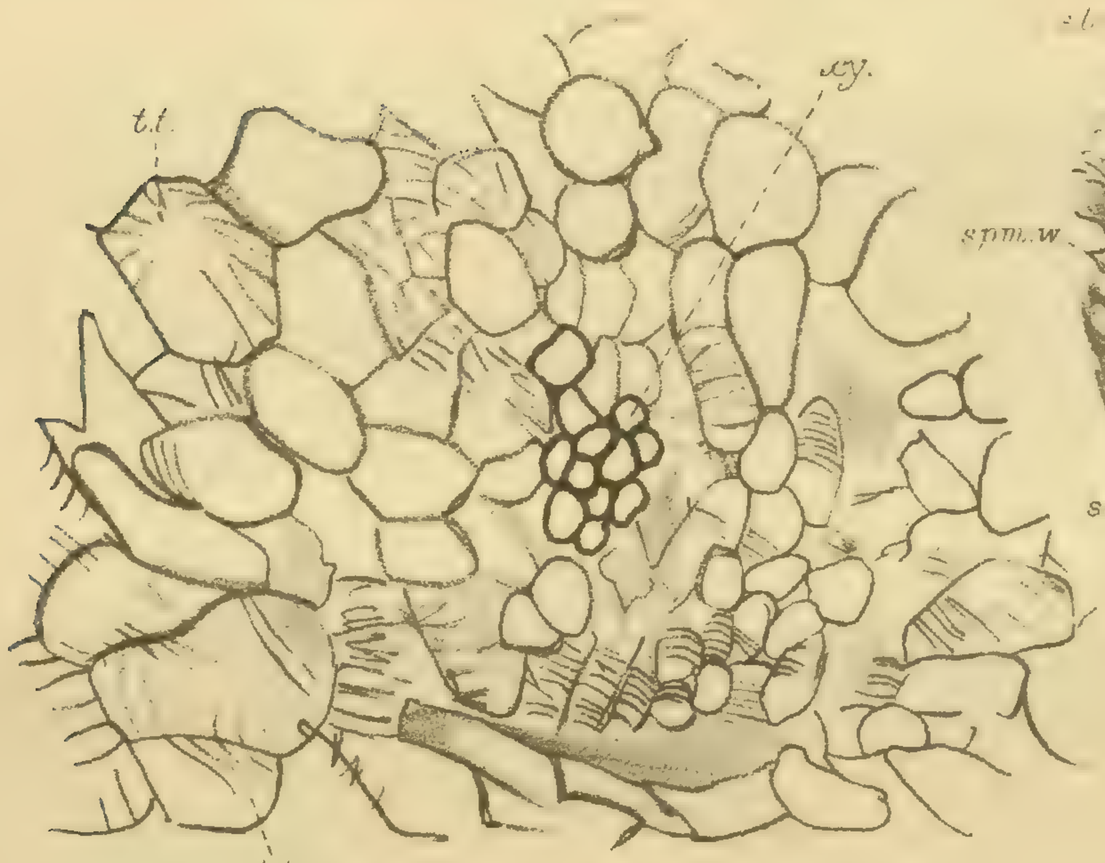
31.



32.



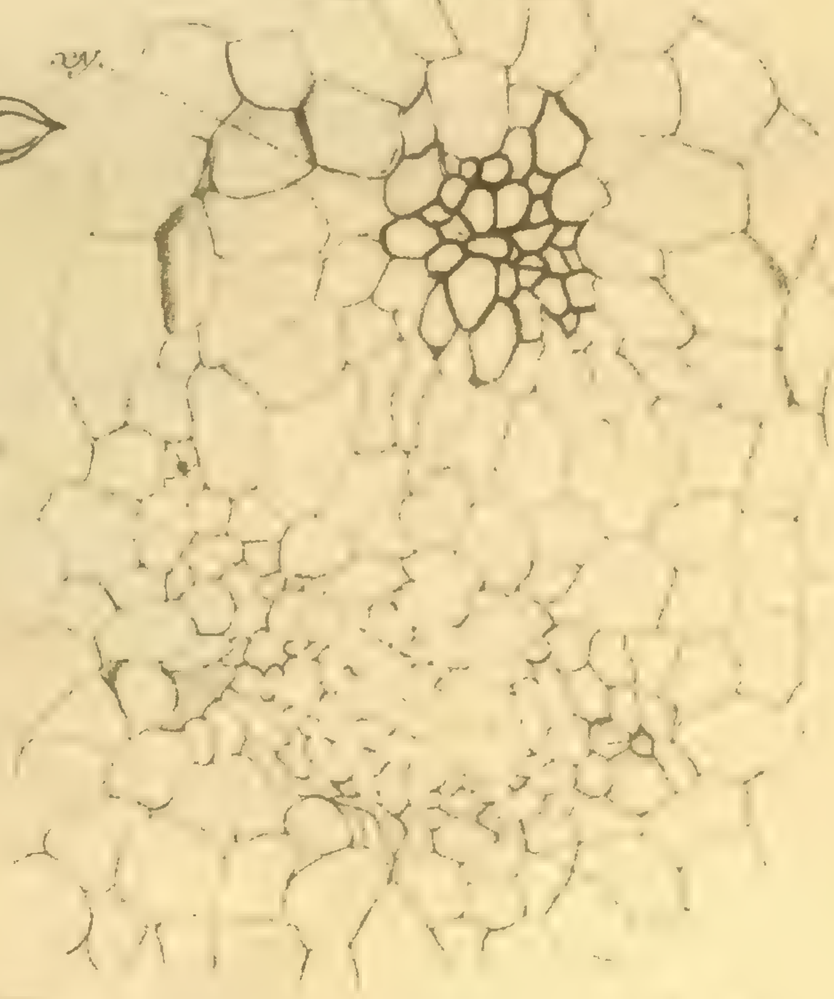
33.



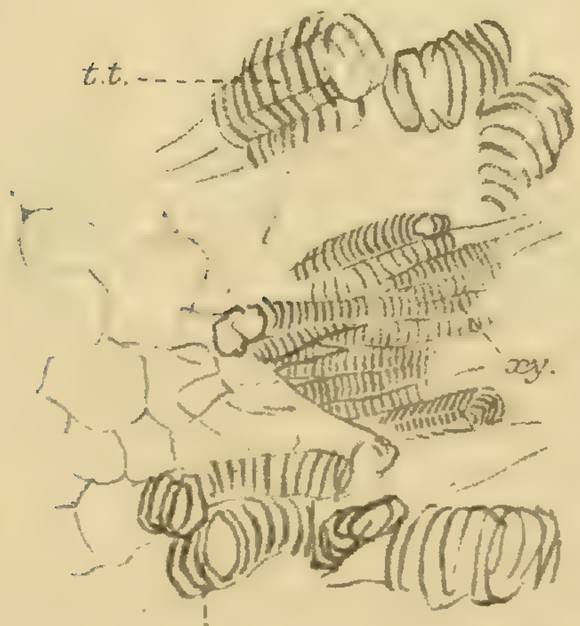
28.

27.

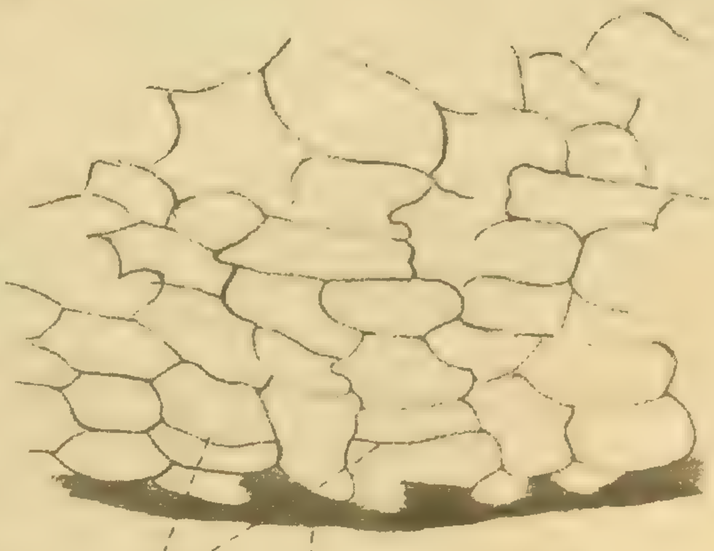
39.



34.

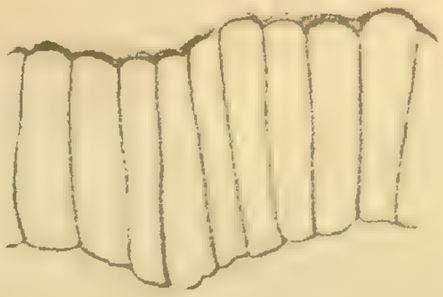


35.



36.

37a.



37b.

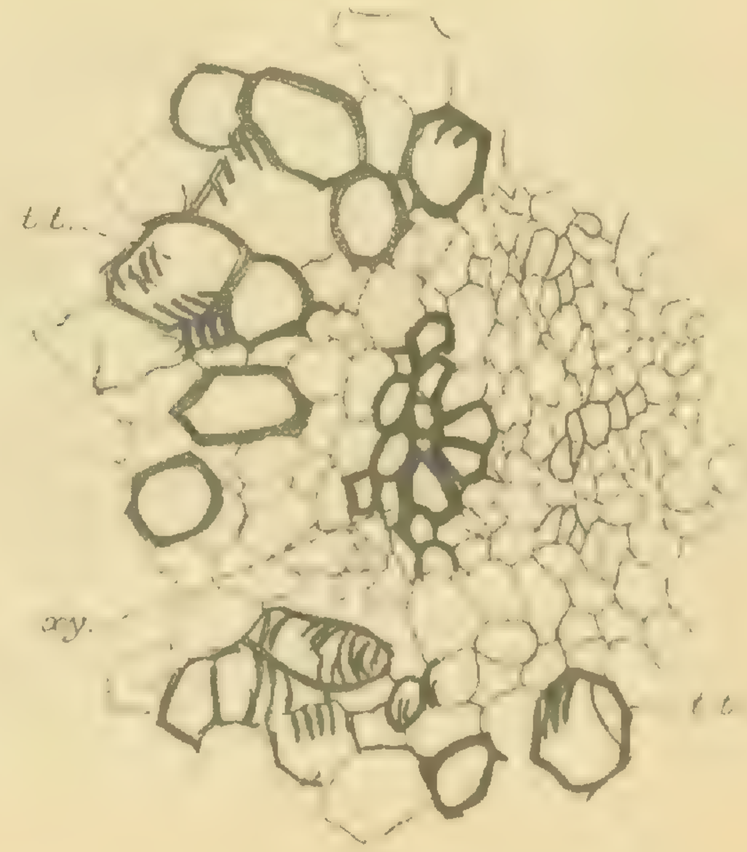
38.

A. Arber del.

Huth, London

LEPIDOSTROBUS BINNEYANUS sp. nova. Figs 26–30, L. GRACILIS sp. nova. Figs 31–39

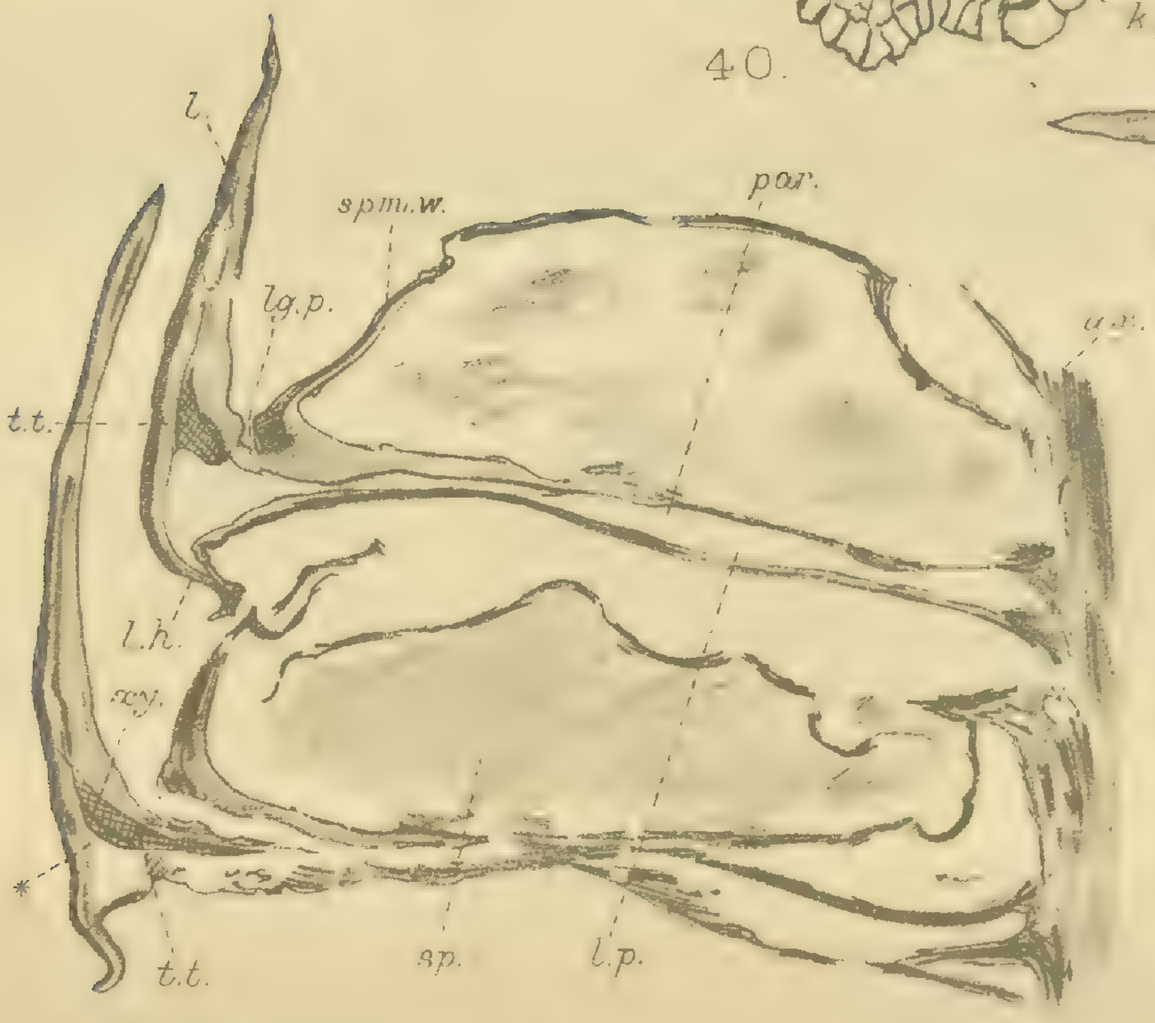
40.



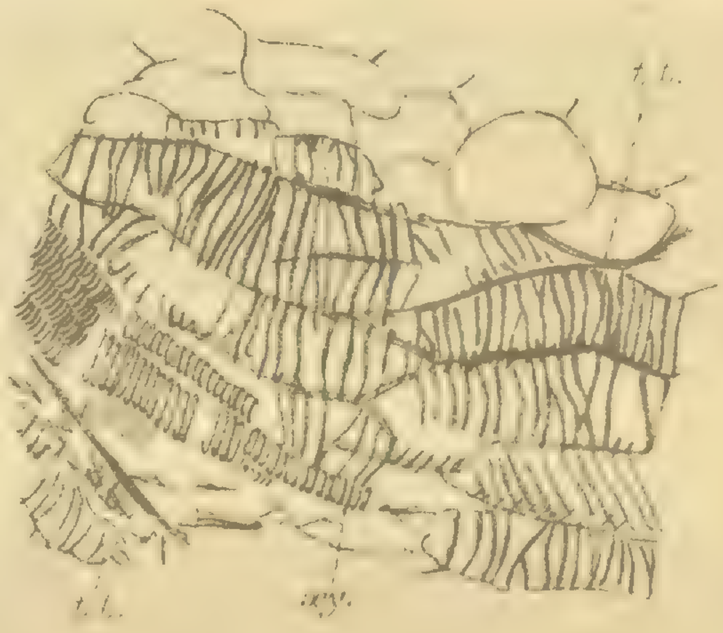
42.

41.

45.

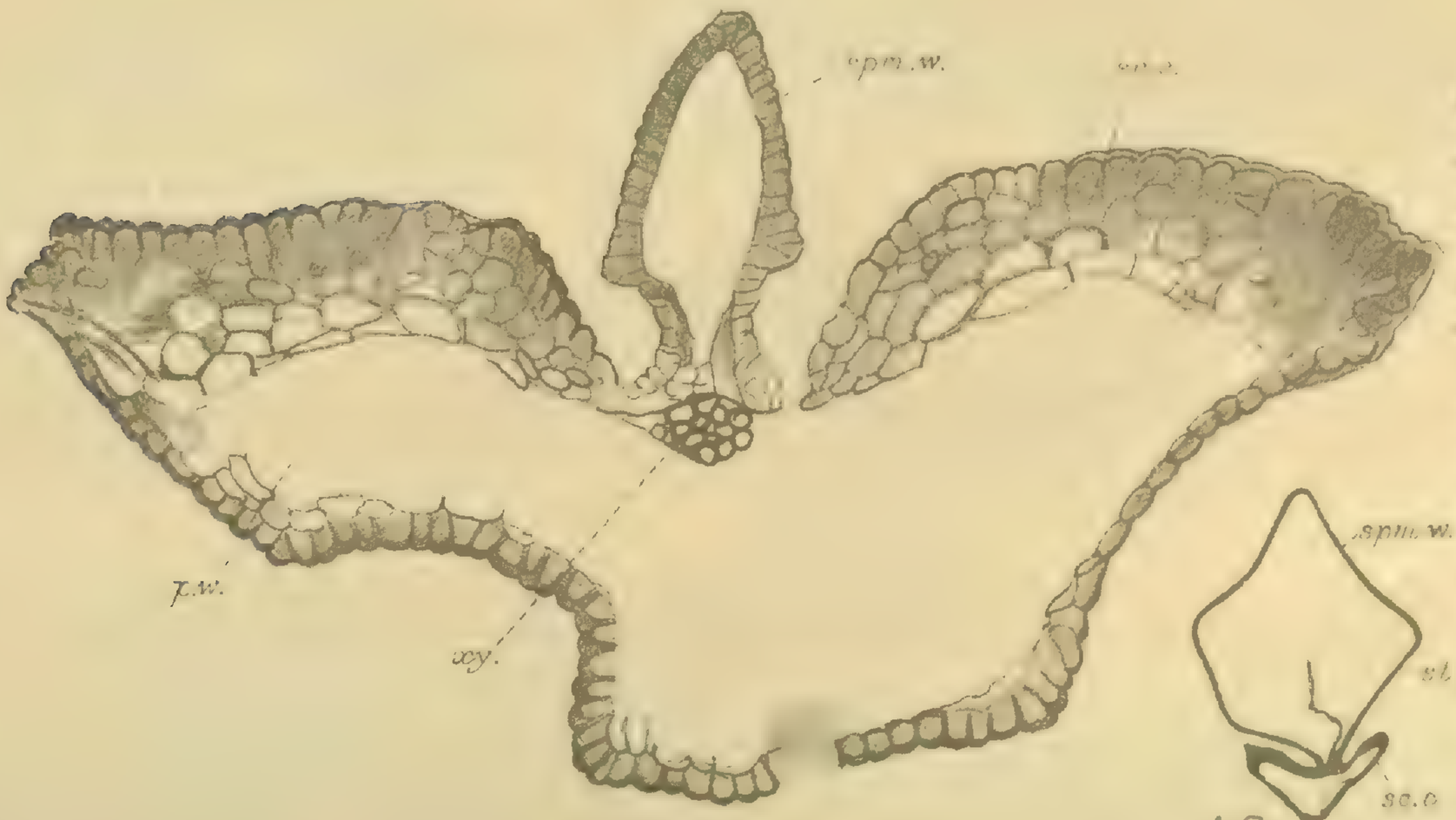


43.

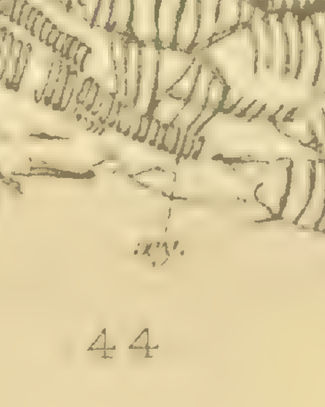


44

49.



47.



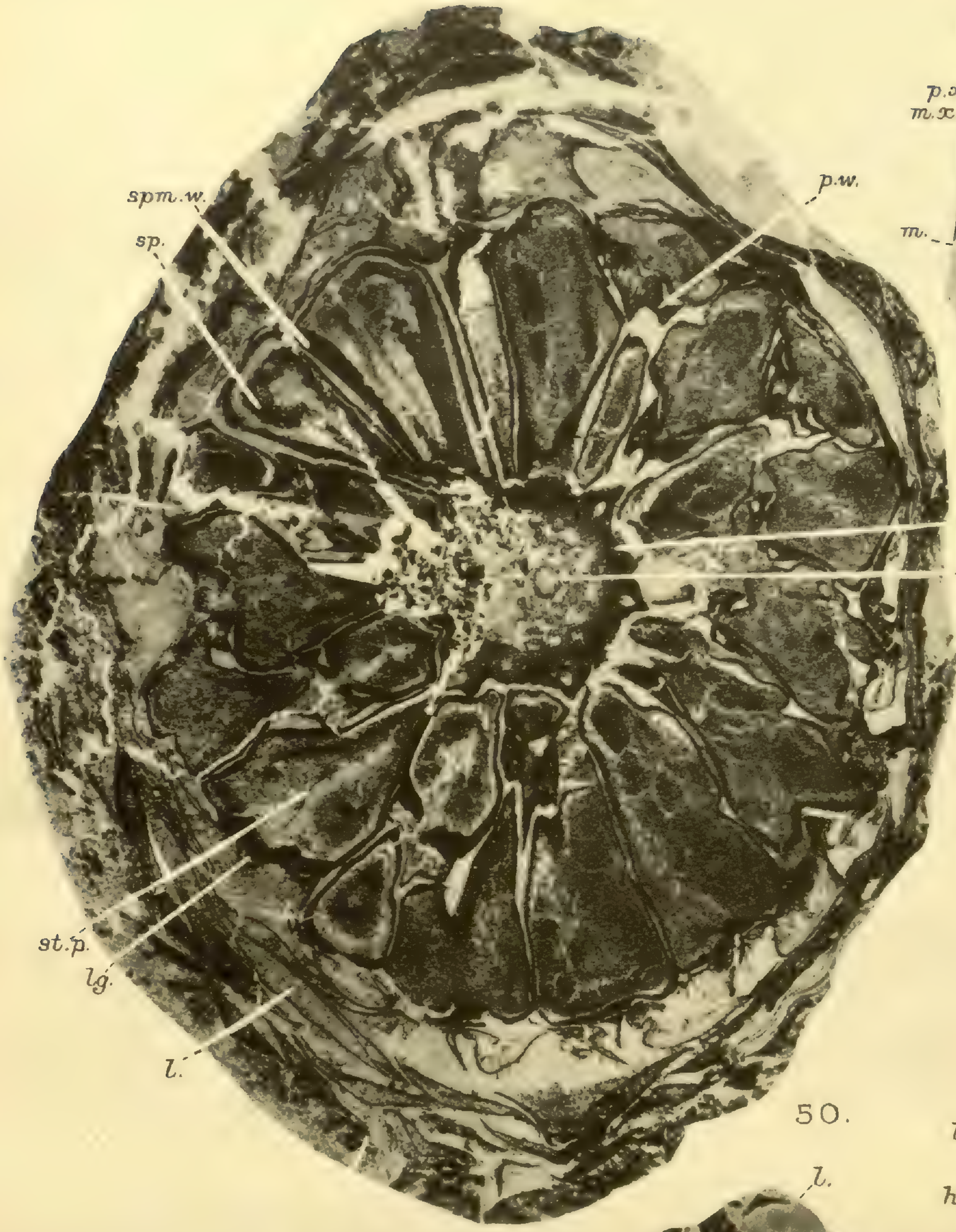
46.

48.

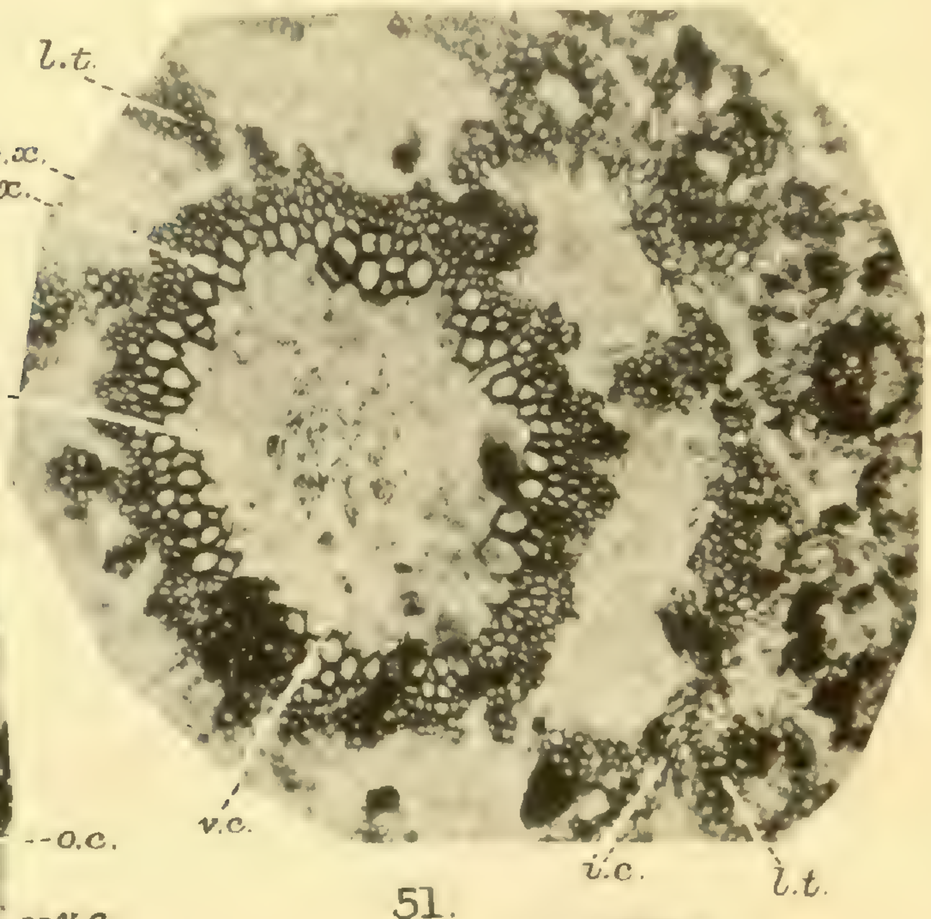
Huth, London.

A. Arber del.

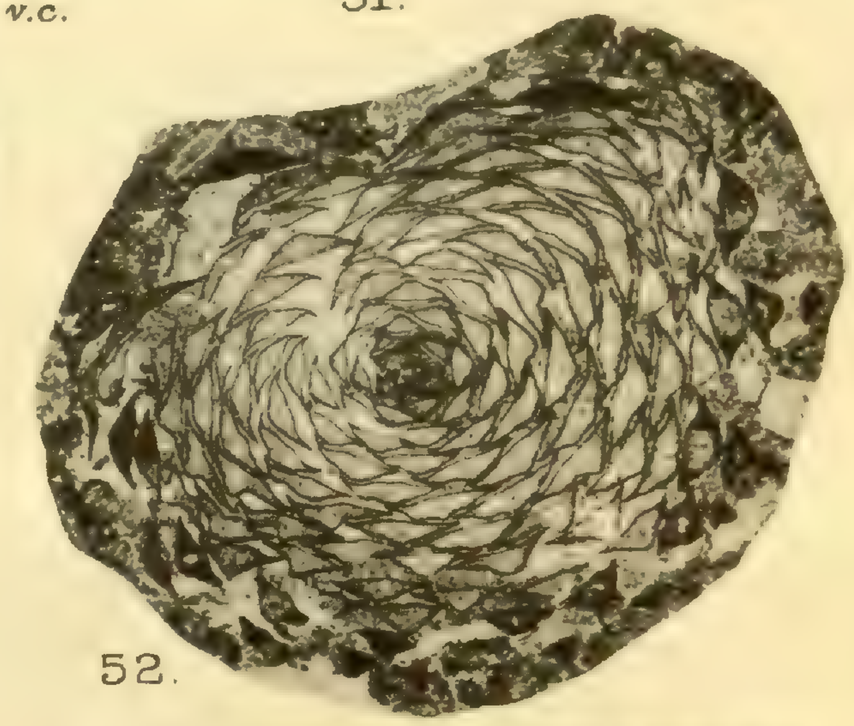
LEPIDOSTROBUS GRACILIS sp. nova. Figs 40–42, L. OLDHAMIUS Will. f. minor Figs 43–49.



50.



51.

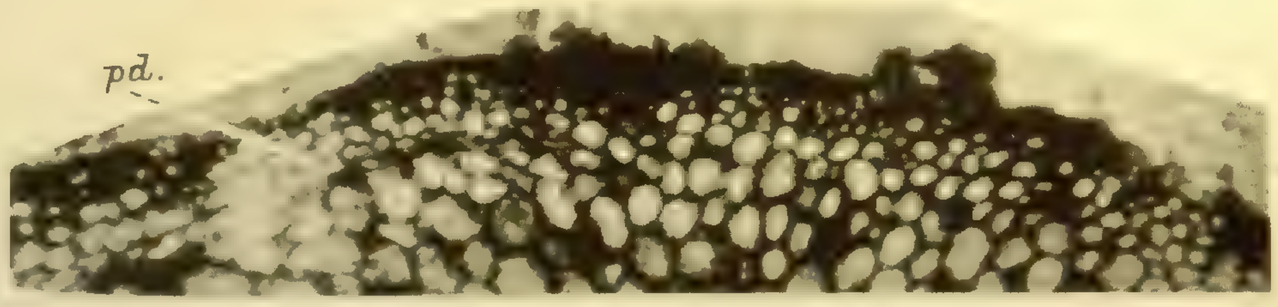


52.

54.

53.

55.



56.

W. Tams phot. Huth coll.

LEPIDOSTROBUS OLDHAMIUS PILOSUS Will. f. sp. nova. Figs 50–54, L. OLDHAMIUS Will. Figs 55, 56.

LINNEAN SOCIETY OF LONDON.

MEMORANDA CONCERNING TRANSACTIONS.

The First Series of the Transactions, containing both Botanical and Zoological contributions, has been completed in 30 Vols., and a few entire sets are still for sale. Only certain single volumes, or parts to complete sets, may be obtained at the original prices. The price of the Index to Vols. 1–25 is 8*s.* to the public, and 6*s.* to Fellows; to Vols. 26–30, 4*s.* to the public, and 3*s.* to Fellows.

The Second Series of the Transactions is divided into Zoological and Botanical sections. The prices of the Botanical parts of these which have been published are as undermentioned. (For the Zoological parts see Zoological wrapper.)

SECOND SERIES.—BOTANY.

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
I.	Parts I.–IX. (complete). 1875–80.	8	1	0	6	1	0
II.	Parts I.–XVI. (complete). 1881–88.	6	16	10	5	2	3
III.	Parts I.–XI. (complete). 1888–94.	7	12	10	5	14	8
IV.	Parts I.–IV. (complete). 1894–95.	5	13	4	4	5	0
V.	Part I. 1895.	0	9	0	0	6	9
	Part II. 1895.	0	12	0	0	9	0
	Part III. 1896.	0	6	0	0	4	6
	Part IV. 1896.	1	0	0	0	15	0
	Part V. 1896.	0	14	0	0	10	6
	Part VI. 1896.	0	4	0	9	3	0
	Part VII. 1897.	0	4	0	0	3	0
	Part VIII. 1897.	0	6	0	0	4	6
	Part IX. 1899.	0	12	0	0	9	0
	Part X. 1899.	0	6	0	0	4	6
	Part XI. 1899.	0	7	0	0	5	3
	Part XII. 1899.	0	12	0	0	9	0
	Part XIII. 1900.	0	1	6	0	1	2
	Part XIV. 1900.	0	3	0	0	2	3
	Part XV. 1901.	0	6	0	0	4	6
VI.	Part I. 1901.	1	10	0	1	2	6
	Part II. 1901.	0	6	0	0	4	6
	Part III. 1902.	0	18	0	0	13	6
	Part IV. 1903.	0	8	0	0	6	0
	Part V. 1903.	0	8	0	0	6	0
	Part VI. 1903.	0	12	0	0	9	0
	Part VII. 1904.	0	12	0	0	9	0
	Part VIII. 1904.	0	12	0	0	9	0
	Part IX. 1904.	0	7	0	0	5	3
	Part X. 1904.	0	14	0	0	10	6
	Part XI. 1905.	0	4	0	0	3	0

SECOND SERIES.—BOTANY (*continued*).

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
VII.	Part I. 1904.	0	5	0	0	3	0
	Part II. 1905.	0	6	0	0	4	6
	Part III. 1906.	0	3	0	0	2	3
	Part IV. 1906.	0	7	0	0	5	3
	Part V. 1907.	0	10	0	0	7	6
	Part VI. 1907.	0	4	0	0	3	0
	Part VII. 1907.	0	6	0	0	4	6
	Part VIII. 1908.	0	5	0	0	3	9
	Part IX. 1908.	0	2	6	0	2	0
	Part X. 1908.	0	7	0	0	5	3
	Part XI. 1909.	0	4	0	0	3	0
	Part XII. 1909.	0	12	0	0	9	0
	Part XIII. 1909.	0	5	0	0	3	9
	Part XIV. 1909.	0	6	0	0	4	6
	Part XV. 1910.	0	6	0	0	4	6
	Part XVI. 1912.	0	3	0	0	2	3
	Part XVII. 1912.	0	8	0	0	6	0
	Part XVIII. 1912.	0	5	0	0	3	9
	Part XIX. 1912.	0	3	0	0	2	3
	Part XX. Index.	0	3	0	0	2	3
VIII.	Part I. 1913.	1	0	0	0	15	0
	Part II. 1913.	0	8	0	0	6	0
	Part III. 1913.	0	8	0	0	6	0
	Part IV. 1913.	0	4	0	0	3	0
	Part V. 1913.	0	10	0	0	7	6
	Part VI. 1914.	0	12	0	0	9	0

2nd Ser. BOTANY.] [VOL. VIII. PART 7.

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

A CONTRIBUTION TO THE STUDY OF THE EVOLUTION OF THE FLOWER, WITH SPECIAL REFERENCE TO THE HAMAMELIDACEÆ CAPRIFOLIACEÆ, AND CORNACEÆ.

BY

ARTHUR SAMUEL HORNE, B.Sc., F.L.S., F.G.S.,

LECTURER ON BOTANY IN THE ROYAL HORTICULTURAL SOCIETY'S SCHOOL OF HORTICULTURE.

(Plates 28–30 and 13 Text-figures.)

LONDON:

PRINTED FOR THE LINNEAN SOCIETY

BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON-HOUSE, PICCADILLY, W.,

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

December 1914.

VIII. *A Contribution to the Study of the Evolution of the Flower, with special reference to the* Hamamelidaceæ, Caprifoliaceæ, *and* Cornaceæ.

By Arthur Samuel Horne, *B.Sc., F.L.S., F.G.S., Lecturer on Botany in the Royal Horticultural Society's School of Horticulture.*

(Plates 28–30 and 13 Text-figures.)

Read 4th December, 1913.

Contents.

	Page
1. Introduction	239
2. Hamamelidaceæ	245
3. Caprifoliaceæ	251
4. Cornaceæ	261
(a) *Cornus*	261
(b) *Alangium* and *Marlea*	265
(c) *Aucuba*	269
(d) *Garrya*	274
(e) *Helwingia*	278
(f) *Corokia*	282
(g) *Melanophylla*	284
(h) *Griselinia*	284
(i) *Nyssa*	287
5. Final Discussion	291

Argument:—The Interpretation of Resemblances and Differences. Origins. Phylogeny of the Hamamelidaceæ. Phylogeny of the Caprifoliaceæ. Phylogeny of the Cornaceæ. The Vascular Structure of the Flower in Angiosperms. The Ovule in Angiosperms. Ovular connections. Ovular Vascular System. The Phylogeny of Angiosperms 291–302

1. INTRODUCTION.

The structure of the flower of *Davidia*, a genus referred to the Cornaceæ in 'Die Natürliche Pflanzenfamilien,' has been already described by the author* in a paper dealing with the structure and affinities of *Davidia involucrata*, published in the 'Transactions of the Linnean Society,' in 1909. During the study of *Davidia* there was occasion to examine the flowers of several genera of Cornaceæ, and in so doing striking structural differences were discovered not only between representative genera of the subfamilies but also between the genera that have been grouped in a particular subfamily, such as, for instance, the Cornoideæ. At the same time, as reference had

* A. S. Horne in Linn. Soc. Trans. 2nd ser., Bot. vii. (1909) 303–326, t. 31–33.

been repeatedly made to the Hamamelidaceæ and Caprifoliaceæ in the attempt to arrive at an interpretation of the floral morphology and a solution of the phylogeny of *Davidia*, it soon became evident that a close scrutiny of the evolutionary tendencies exhibited by these families would lead to a broader conception of the significance of the new discoveries, and shed considerable light upon the origin of the flower in several genera of Cornaceæ. Influenced by these considerations, the author has undertaken an elaborate and extended investigation of the Hamamelidaceæ, Caprifoliaceæ, and the Cornaceæ (as defined by Harms), notwithstanding the fact that these families are arranged in different cohorts in Engler's System—with the object of elucidating the true phylogeny of the Cornaceæ, and in the belief that the investigation would have a direct bearing upon the whole question of the phylogeny of the Angiosperms.

It is the object then of the present paper to record the facts that have been observed, and to present the conclusions that have been deduced from a comparative study of the evolutionary changes which are evident among the Hamamelidaceæ, Caprifoliaceæ, Cornaceæ, Araliaceæ, and other nearly associated families.

The composition of the family Hamamelidaceæ varies but little in the chief systematic works. Of the eighteen genera enumerated by Niedenzu *, in 'Die Pflanzenfamilien,' fifteen are recorded by Bentham and Hooker †, sixteen by Baillon ‡, and nine of the ten genera known to science at the time, by Endlicher §. Our knowledge of the general morphology is largely due to Baillon's ‖ researches, which are described in 'Adansonia.' Daniel Oliver ¶ contributed a valuable paper on *Sycopsis*, a new genus of Hamamelidaceæ, in 1860, and a note ** relating to the structure of the anther in *Hamamelis* and *Loropetalum* in 1862. The embryology of several genera was studied by Shoemaker †† in 1905.

The composition of the family Caprifoliaceæ has also varied little in the different systems. Of the eleven genera enumerated by Fritsch ‡‡ in 'Die Pflanzenfamilien,' all are recorded by Bentham and Hooker, and nine by Endlicher. *Adoxa*, appearing in Bentham and Hooker's list, is not retained by Fritsch. F. Höck §§ proposed the transference of *Sambucus* to a new family, the Sambucaceæ, but his suggestion has not received general acceptance.

The literature is chiefly systematic, or of a strictly morphological character. Maximowicz ‖‖ contributed an extensive monograph on the Caprifoliaceæ to the 'Bulletin de l'Académie Impériale des Sciences de Saint Pétersbourg.' Oersted ¶¶ revised the grouping

* F. Niedenzu in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 2*a* (1891) 115–130.

† G. Bentham et J. D. Hooker, Gen. Pl. ii. 664–669.

‡ H. Baillon, Histoire des Plantes, iii. (1872) 456–461.

§ S. Endlicher, Gen. Pl. (1836–1840) 803.

‖ H. Baillon in Adansonia, i., v., xi.

¶ D. Oliver in Linn. Soc. Trans., Bot. xxiii. (1860) 83.

** D. Oliver, *l. c.* (1862) 457.

†† D. N. Shoemaker in Bot. Gaz. xxxix. (1905) 248.

‡‡ Fritsch in Engl. u. Prantl, Nat. Pfl., Teil iv. Abt. 4 (1891) 156.

§§ F. Höck in Bot. Centr. li. (1892) 233.

‖‖ C. J. Maximowicz in Bull. Acad. Imp. Sci. St. Pétersbourg: xxiv., *Lonicera* (1878); xxvi., *Viburnum* (1880); xxvii., *Triosteum* (1881); xxxi., *Linnæa*, *Diervilla* (1887).

¶¶ Oersted in Vidensk. Meddel. Naturh. Foren. Köbenh. vi. & vii. (1861) 267–305.

of the species of *Viburnum*, according to the character of the fruit, in 1861. E. A. Newell Arber * interpreted several cases of synanthy in *Lonicera*, in 1903. The embryology of the family has been neglected since the records that appear in the memoirs of Hofmeister † (1858, 1859), Vesque ‡ (1878, 1879), and Guignard § (1882).

The composition of the family Cornaceæ, unlike that in the above-mentioned families, does vary considerably in different systems. With the object, therefore, of making the exposition more intelligible, a table (see p. 242) has been drawn up, to collate the classification of the Cornaceæ adopted by Harms in 'Die Pflanzenfamilien' with those of other systematists.

It will be noted that the genera aggregated by Harms in the Cornaceæ were distributed among several families in the systems of Endlicher, De Candolle, and Lindley; thus the Cornaceæ comprise only five genera in De Candolle's ‖ 'Prodromus' (*Cornus*, *Aucuba*, *Griselinia*, *Mastixia*, and *Curtisia*); while other genera known to science at the time were segregated in the families Garryaceæ, Alangiaceæ, Helwingiaceæ, and Araliaceæ.

Benjamin Clarke ¶ described some observations upon the flowers of *Marlea* in a paper contributed to Hooker's 'Journal of Botany' so long ago as 1850, and came to the conclusion that the Alangieæ (*Alangium* and *Marlea*) are closely related to *Cornus*. Clarke's paper seems to have been overlooked.

Bentham and Hooker** include the Corneæ, Alangieæ, Garryaceæ, and Nyssaceæ of earlier systematists in the Cornaceæ. They define the Cornaceæ in terms of the ovule. Thus the genera are characterized by possessing ovules of the ventral type (with dorsal raphe), in contradistinction to the Araliaceæ where the ovules are of the dorsal type (with ventral raphe). But this criterion has proved to be unsound for two reasons: first, because the structure of the ovule in certain genera (*Helwingia*, *Nyssa*) was at the time imperfectly known, and, secondly, in that the so-called dorsal ovules are not necessarily homologous and do not strictly conform to a single type.

Baillon †† contributed important additions to our knowledge of the morphology of the family. He was the first to point out the peculiar morphology of the supposed calyx in *Garrya*, and worked out the development ‡‡ of the flower in both *Garrya elliptica* and the hybrid, *Garrya Thuretii*. But his interpretations of floral structure and affinities in the Cornaceæ were profoundly influenced by the results accruing from his researches §§ relating to the organogeny of the flower in the Amentiferæ. He found

* E. A. Newell Arber in Journ. Linn. Soc., Bot. xxxv. (1903) 463–474.

† W. Hofmeister in Pringsh. Jahrb. i. (1858) 120–121; and in Abhandl. Königl.-Sächs. Gesell. Wiss. (1859), 533–672, t. 1–27.

‡ J. Vesque in Ann. Sci. Nat., Bot. 6me sér. vi. (1878) 237–285, viii. (1879) 261–390.

§ Guignard in Ann. Sci. Nat., Bot. 6me sér. xiii. (1882) 136–198.

‖ A. de Candolle, Prodromus, iv. (1830) 271.

¶ Benjamin Clarke in Hooker's Kew Journ. vol. ii. (1850) 129.

** Bentham et Hooker, 'Genera Plantarum,' vol. i. part iii. (1867) 947.

†† H. Baillon in Adansonia, v. (1864) 179–203; x. (1871–1873) 112–117.

‡‡ H. Baillon in Bull. Soc. Linn. Paris (1877), 139.

§§ H. Baillon in Adansonia, xi. (1873–1876) 163–174; xii. (1876–1879) 1–20.

TABLE I.—THE ARRANGEMENT OF THE CORNACEÆ OF HARMS IN OTHER SYSTEMS.

Wangerin, 1910 *.		Harms, 1898 †.	Baillon, 1877–1879 ‡.	Bentham & Hooker, 1867 §.	Endlicher, 1847 ‖.	Lindley, 1847 ¶.	Endlicher, 1836–1840 **.	De Candolle, 1830 ††.
Garryaceæ.	I.	Garrya.	Cornaceæ ser. II.	Cornaceæ sec. II.	Garryaceæ.	Garryaceæ.	Garryaceæ antedesmeis affines.	Garryaceæ.
Nyssaceæ.	II.	Nyssa.			Nyssaceæ.	Alangiaceæ.	Nyssaceæ; genera Santalaceis affinia.	— —
		Camptotheca.			— —	— —	— —	— —
	III.	Davidia.	Combretaceæ.	— —	— —	— —	— —	— —
Alangiaceæ.	IV.	Alangium.		Cornaceæ sec. I.	Corneæ.	Alangiaceæ.	Alangieæ.	Alangiaceæ.
		Marlea.						
Cornaceæ.	V.	Mastixia.	Umbelliferæ.		Corneæ Aucubeæ.	Cornaceæ?	genera dubia Cornaceis affinia cum Polyosmate Votomita.	Corneæ.
	VI.	Curtisia.	(Araliæ.)		Corneæ veræ.			
	VII.	Helwingia.	Cornaceæ ser. I.	Araliaceæ.	Helwingiaceæ.	Helwingiaceæ.	Helwingiaceæ; genera Santalaceis affinia.	Helwingiaceæ.
		Corokia.			Corneæ Aucubeæ.	Cornaceæ.	genera Rhamnaceis affinia.	— —
		Cornus.		Cornaceæ sec. I.	Corneæ.		Corneæ.	Corneæ.
		Benthamia.			Corneæ veræ.			
		Toricellia.			Araliaceæ.	Araliaceæ.	Araliaceæ.	Araliaceæ.
		Melanophylla.	— —	— —	— —	— —	— —	— —
		Kaliphora.	Cornaceæ ser. I.	Cornaceæ sec. II.	— —	— —	— —	— —
		Aucuba.			Corneæ Aucubeæ cum Quadriala & Decostea.	Cornaceæ.	genera Corneis affinia cum Decostea.	Corneæ.
		Griselinia.			Araliaceæ.	— —	genera dubiæ sedis.	— —

* W. Wangerin in 'Das Pflanzenreich,' 41 Heft, 1910.
† Harms in Engl. u. Prantl, Nat. Pfl. Teil iii. Abt. 8, 1898.
‡ H. Baillon, Histoire des Plantes, vii. 1879 (Cornaceæ and Umbelliferæ), and vi. 1877 (Combretaceæ).
§ G. Bentham et J. D. Hooker, Gen. Pl. i. pt. iii. (1867).
‖ S. Endlicher, Gen. Suppl. iv. pts. ii. & iii. 1847.
¶ J. Lindley, The Veg. King. 2nd ed. 1847.
** S. Endlicher, Gen. Pl. 1836–1840.
†† A. De Candolle, Prodr. iv. 1830.

that the ovary of *Quercus*, *Castanea*, and other genera becomes multilocular during development, owing to the inward or centripetal growth of the parietal placentæ, and, hence, was led to the belief that the bilocular ovaries found in certain genera of Cornaceæ originated from unilocular types. But the ovary, in Cornaceæ, as will be subsequently shown, has advanced beyond the evolutionary phase described by Baillon for the Amentiferæ, and presents instead advanced stages in progressive abortion.

Harms * brings together the largest grouping of genera ever included in the Cornaceæ. He asserts that intermediate forms exist between ovules of the dorsal and ventral types, and hence there is no adequate reason for excluding genera with the Aralian type of ovule (*Nyssa* and *Davidia*) from the Cornaceæ. But Harms's opinions carry little weight, owing to the fact that the criteria upon which he relies are insufficient to express the diverse structural forms of ovule obtaining in this family.

Walther Wangerin † contributed a lengthy paper, entitled "Die Umgrenzung und Gliederung der Cornaceæ," to Engler's 'Jahrbücher,' in 1906. This paper describes in detail the chief morphological and anatomical characters of the family, gathered from the works of Sertorius, Baillon, and others, and from an examination of herbarium material. This paper forms the basis of Wangerin's monograph ‡ contributed to 'Das Pflanzenreich' in 1910. The Cornaceæ of Harms are, in this monograph, resolved into four old families, the Garryaceæ, Alangiaceæ, Nyssaceæ, and Cornaceæ. Two of these, the Nyssaceæ (*Nyssa* and *Davidia*) and Alangiaceæ, according to Wangerin, are distinguished by two integuments. The present author §, however, recorded only a single integument for *Davidia* in 1909, and is now able to show that *Nyssa* also is unitegumentary. Hence Wangerin has relied upon a morphological error with regard to the Nyssaceæ, and, in consequence, has failed to present a convincing case for the re-establishment of both families.

The present investigation reveals several hitherto-unrecorded details in the floral organization, the special morphology of the ovary and ovule, and the course of the vascular tissue in the families under consideration. A striking evolutionary series has been traced in the Caprifoliaceæ, where, owing to progressive abortion, the *parietal portion of the ovary* that is well represented in *Leycesteria* has become reduced until, in *Sambucus*, only vestiges remain. Progressive abortion, in the Caprifoliaceæ, is accompanied by progressive sterilization—the ovules are not only reduced in number, but transitional stages occur from ovules physiologically sterile to be found in *Lonicera* to the merest rudiments discovered in *Sambucus*. Owing to reduction the ovary or loculus, in several genera, becomes monospermous, with a terminal seed, but in each case the one-seeded condition has been attained by a different method. Comparison with an analogous sterilization series in the Hamamelidaceæ shows that the terminal seed in the Caprifoliaceæ is constantly axially suspended, or in the exceptional case of *Viburnum* axially borne by origin, whereas in the latter family it is situated parietally.

* Harms in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 8.

† W. Wangerin in Engl. Bot. Jahrb. Band xxxviii. Heft 2 (1906).

‡ W. Wangerin in Engl. Das Pflanzenreich, Heft 41 (1910).

§ A. S. Horne in Trans. Linn. Soc. ser. 2, Bot. vii. (1909) 323.

Passing then to the Cornaceæ, the author selected *Corokia* and *Marlea*, genera with unilocular or bilocular ovaries, and traced the structural changes accompanying the reduction from two loculi to one. With the aid of all the available facts it was then possible to analyse and interpret the uniovulate Cornaceæ, and the single terminal ovule was found to be of multiple origin. The sterilization series evident in the Caprifoliaceæ extends by way of *Sambucus* to the Cornaceæ, where vestiges of ovules are unknown, and the conclusion reached that the ovaries or loculi of the Cornaceæ were primitively pluriovulate is supported by the direct evidence deduced from their own structural peculiarities.

A series has been traced in the direction of the loss of carpellary autonomy by way of the Araliaceæ, Caprifoliaceæ, and Cornaceæ that culminates in the reduced ovary of *Aucuba*, which in appearance and structure simulates a single inferior carpel.

Structural synthesis in the flower is accompanied by a corresponding economic advance in the development of the vascular system. The dorsal and lateral bundles of the carpels, and the traces of the perianth and stamens that exist as independent series in *Aralia* are in the Caprifoliaceæ represented by one series, and the latter family exhibits a still further economical advance reaching in *Viburnum* the condition obtaining in the Compositæ, where the bundles in the single series are reduced to half the sum of the petals and stamens. Two lines of advance towards the evolution of the single series have been traced, one presented by *Aralia*, *Davidia*, and *Marlea*, and the other exemplified by the Hamamelidaceæ.

The ovule in the Caprifoliaceæ and Cornaceæ has advanced far beyond the evolutionary stage exhibited by the Hamamelidaceæ, but whereas there is little deviation from a single type in either the Hamamelidaceæ or Caprifoliaceæ, the ovules of Cornaceæ present diverse forms and structures. The nucellus of Cornaceæ presents some resemblance to that of the Rosaceæ on the one side, and on the other through *Helwingia* to the reduced nucellus of *Lilium* or *Inula*.

Considerable emphasis is laid upon the fact that similar stages and methods of floral construction recur, not only in the same but different families, and upon the fact that similar ends are attained in the same or different families by dissimilar methods. The separation of the sexes occurs in several genera of Hamamelidaceæ, Rosaceæ, and numerous other families. Epigynous structures have arisen in numerous groups and even in the same group by more than one device. The centripetal development of parietal placentæ, rendering the ovary multilocular, occurs in *Castanea*, *Quercus*, *Rhodoleia*, and many other genera. Similar stages in the evolution of the vascular system have recurred in *Castanea*, the Caprifoliaceæ, and Cornaceæ, whilst similar arrangements of ovules are found and the details of the vascular supply are nearly identical in different families. Neither is the ovule by any means exempt. The separation of one type from another; the transition from bi- to unitegumentary forms, and the evolution of the exalbuminous seed has happened again and again in the racial experience of Angiosperms. Convergence and parallel development are established doctrines, but many authors have failed to grasp their significance. Convergence in

one or a few characters may not prove of much importance, but when the action of evolutionary forces has achieved a like resultant or effect, and similar combinations of characters are found, the problem of origins becomes almost insoluble.

The author is led, from the facts presented here, to express the strong conviction that the structural peculiarities to be perceived in both the Caprifoliaceæ and Cornaceæ are indicative of different origins; that certain genera in each family have pursued independent but similar lines of development, and hence both families are convergent and polyphyletic. The case for the polyphyletic origin of Cornaceæ has already been stated before the Botanical Section of the British Association at Portsmouth in 1911 *.

The author, in conclusion, indicates the bearing of modern experimental work upon the field of enquiry pursued here, discusses the affinities of the three families specially studied, outlines the general features in the evolution of the floral vascular system and of the ovule, and, finally, sums up the position created by this investigation in relation to the natural classification of Angiosperms.

This research was commenced at the Royal College of Science, London, and finished at the Wisley Laboratory, and my thanks are due to the President and Council of the Royal Horticultural Society and the Director of the Laboratory for the opportunities they have given me for pursuing my study on this subject at Wisley.

I am chiefly indebted to Professor J. B. Farmer, F.R.S., and to Mr. A. W. Hill, F.L.S., Assistant Director of the Royal Botanic Gardens, Kew, for the material used. Specimens of *Griselinia lucida* were kindly collected and preserved for the purpose of this investigation by Miss Heywood, in New Zealand, at the request of Dr. O. V. Darbishire; and flowers of *Griselinia littoralis* were contributed by Mr. J. W. Hamilton of Hamwood, Dunboyne, Ireland. For the rare female catkins of *Garrya elliptica*, the author is indebted to Messrs. Veitch, and inflorescences of several rare Caprifoliaceæ were obtained from the Gardens of the Royal Horticultural Society.

2. HAMAMELIDACEÆ.

Since the writer aims at a comparison of origins, considerable importance is attached to details of floral organization, and for this reason special attention is given to variability in the position occupied by the ovary in relation to the remaining floral whorls, to details in the internal structure of the ovary, to the number and structure of the ovules, and to sterilization in the ovary; special interest also attaches to an instance of the transformation of the petals into stamens that he has observed in *Corylopsis* and to the elucidation of the morphology of the bracts found in *Parrotia*, whilst the course of the vascular tissue in the flower has also been traced.

The variability in the position occupied by the ovary in relation to the outer whorls will be considered first. *Distylium* is hypogynous, *Hamamelis* and *Corylopsis* are perigynous, and the perianth and stamens are seated upon a circular ridge of tissue attached to the ovary below mid-height. *Trichocladus* also is perigynous, but the ridge

* A. S. Horne in Proc. Brit. Assoc. Adv. Sci. Portsmouth (1911), p. 585.

is inserted at a higher level. *Eustigma*, from the illustration accompanying Seeman's * "Botany of the Voyage of H.M.S. 'Herald,'" is subepigynous. Thus the ovaries of the above-mentioned genera fall into a complete series varying from a hypogynous to an epigynous structure. *Sycopsis*, as originally noted by D. Oliver †, differs from all the remaining Hamamelidaceæ. Oliver states that the ovary appears to be inferior, owing to the fact that it is surrounded by a closely adpressed tube, which bears at its margin the remaining floral whorls. He remarks that when the tube is laid open by dissection the ovary is clearly superior. Hence *Sycopsis* forms the only other member of a second series, beginning with a *Distylium*-like form in which the perigynous ridge has become specially developed and adpressed to the ovary-wall. Very frequently, organs originally adpressed become congenitally united, so that the step from the structure in *Sycopsis* to a truly epigynous flower is not a great one. *Loropetalum* is epigynous, according to the figures of *Hamamelis chinensis* given by Robert Brown in Abel's ‡ 'Narrative of a Journey to China' and to the published illustration of *Loropetalum chinense* §. The probable origin of the epigynous condition has not yet been investigated. In proceeding to pass in review the structure of the ovary itself, it may be remarked that the Hamamelidaceæ are divided by Niedenzu ‖ into two subfamilies, the Bucklandioideæ (ovaries with pluriovulate loculi) and the Hamamelidoideæ (ovaries with uniovulate loculi)—a method of grouping that corresponds to the one adopted by Endlicher ¶ in 1836. Now the ovary of *Rhodoleia*, a genus of the Bucklandioideæ, is specially noteworthy: that of *R. Championi* is described as bilocular in Walpers's ** 'Annales Botanices Systematicæ' and in Curtis's †† 'Botanical Magazine,' but Bentham ‡‡, in his 'Flora Hongkongensis,' records that it consists of two carpels united at the base into a one-celled ovary with parietal placentæ. Baillon §§ states that the ovary of *Rhodoleia* is either completely or incompletely two-celled, that it is especially incomplete below, where often the placentæ do not even touch; that in the Sumatran species (*R. Teysmannia*) they are more or less fused higher up, but in the Chinese (*R. Championi*) they are only in contact and may be separated without rupture; thus they are really parietal as in so many of the Saxifragineæ. J. G. Boerlage ‖‖, in 'Flora van Nederlandsch Indie,' records that the ovary is bilocular and sometimes unilocular owing to the disappearance of the dissepiment, and, finally, Niedenzu ¶¶ states that it is either

* Seeman, Botany of the Voyage of H.M.S. 'Herald,' Tab. 95.

† D. Oliver in Trans. Linn. Soc., Bot. xxiii. (1860) 83; *Sycopsis sinensis* in Hook. Ic. 1931 (1891).

‡ Robert Brown in Abel's 'Narrative of a Journey to China,' fig. 4.

§ In Icon. Select. Horti Thenen. pl. 58. fig. 8.

‖ Niedenzu in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 2 (1891) 121.

¶ S. Endlicher, Gen. Pl. (1836–1840) 803.

** In Walpers's 'Annales Botanices Systematicæ,' Tom. iii. 842 (1850–1853).

†† In Curtis's Bot. Mag. vi. Tab. 4509 (1850).

‡‡ Bentham, 'Fl. Hongkongensis,' p. 131 (1861).

§§ H. Baillon, Histoire des Plantes, iii. 393 (1872).

‖‖ J. G. Boerlage, 'Flora van Nederlandsch Indie,' i. Polypetalæ, 454 (1890).

¶¶ Niedenzu, *l. c.* p. 122; fig. 68 (p. 123).

unilocular, completely bilocular, or bilocular in the superior portion only. The above-mentioned descriptions appear to the writer to afford clear evidence that the ovary of *Rhodoleia* is varying in the degree of centripetal development of the placentæ, and in so doing exhibits a tendency to break into different types distinguished by the presence and absence of a septum respectively. The ovaries of the Hamamelidoideæ possess a septum which renders them bilocular.

The ovules in the Bucklandioideæ are arranged in series attached, in unilocular forms of *Rhodoleia*, to parietal placentæ. In *Liquidambar*, according to Shoemaker *, they are developed on marginal placentæ. The writer attaches some importance to the method of placentation in the Hamamelidoideæ. Sargent † states that the ovules in *Hamamelis* are suspended from the septum. Niedenzu ‡ gives a representation of them attached to the septum in *Hamamelis* and *Corylopsis spicata*, but the writer, after a careful examination of several species (notably, *Hamamelis virginica*, *arborea*, and *Zuccariniana*, *Corylopsis spicata*, *Parrotia Jacquemontiana*, and *Fothergilla Gardeni* and *major*), finds that they are not thus attached, but borne upon parietal placentæ that are situated immediately above the septum.

There are some interesting points connected with the number of ovules, and it is possible to arrange certain genera in a series from those in which the ovules are numerous in each loculus to those with uniovulate loculi. Shoemaker § records two series in each loculus of *Liquidambar styraciflua*. Le Maout and Decaisne ‖ note that the ovules of the Hamamelideæ (including *Bucklandia*) are either solitary or numerous, but in the latter case only the lower are fertile, whilst in *Disanthus cercidifolius*, from Baillon's ¶ description, the number of ovules in each series is reduced to three. Reduction reaches an extreme in the Hamamelidoideæ. Here it is generally stated that the ovaries possess uniovulate loculi, although Baillon ** long ago described two instances in which the loculi are, at first, biovulate, but later uniovulate, owing to the arrestment of one of the pair, thus in *Hamamelis virginica*, "Dans l'angle interne de chaque loge, il y a un placenta vers le haut duquel s'insérent un ou deux ovules descendants. Dans ce dernier cas, l'un d'eux s'arrête de bonne heure dans son développement"; and in *Distylium* "Il y a dans chaque loge deux ovules dont un seul prend tout son développement." Le Maout and Decaisne †† even figure a four-seeded fruit of *Hamamelis*. Shoemaker ‡‡ found only one example of an ovary with biovulate carpels in *H. virginiana*, although he examined several hundred flowers and suggests

* D. N. Shoemaker in Bot. Gaz. xxxix. (1905) 262.
† Sargent, Silva of N. Amer. v. (1893) 1.
‡ Niedenzu in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 2 (1891), figs. 65 (*Hamamelis*) and 72 (*Corylopsis spicata*).
§ D. N. Shoemaker, *l. c.* 262.
‖ Le Maout and Decaisne, Gen. Syst. Bot. ed. Hook. 410 (1876).
¶ H. Baillon, Histoire des Plantes, iii. 396 (1872).
** H Baillon, *l. c.* 390 (*Hamamelis*); 395 (*Distylium*).
†† Le Maout and Decaisne, *l. c.* 409.
‡‡ D. N. Shoemaker, *l. c.* 251.

that the condition described by Baillon may occur more frequently in places from which he had not obtained material. The writer has hitherto failed to find even traces of a second ovule in *H. virginica*, *Zuccariniana*, and *arborea* (Text-fig. 1, A 3, A 4), but he has observed biovulate loculi in *Fothergilla Gardeni* and *major*, *Corylopsis spicata*, and *Parrotia Jacquemontiana* (Text-fig. 1, C 2). Parallel instances to these occur among the Araliaceæ and Umbelliferæ: thus two ovules suspended from terminal parietal placentæ develop in each loculus of *Aralia* and *Acanthopanax* and, according to Tanfani *, of *Apium*; and one of each pair aborts as it does in the Hamamelidoideæ cited above.

According to Baillon's † description, reduction in the ovary proceeds still further, thus in *Hamamelis* the ovary is sometimes completely sterile:—"Dans un grand nombre de fleurs, le gynécée demeure petit, stérile, on ne renfermant que des rudiment d'ovules"; again, in *Corylopsis*, "Il y a tous les passages quant au gynécée entre des ovaires complètement stériles et vides; et ceux que contiennent des ovules bien constitués, dans les fleurs femelles ou hermaphrodites." Here, in two distinct genera, separation of the sexes is recorded as actually taking place, a feature highly significant when it is remembered that several genera of Hamamelidaceæ possess polygamous flowers and in certain others the flowers are unisexual.

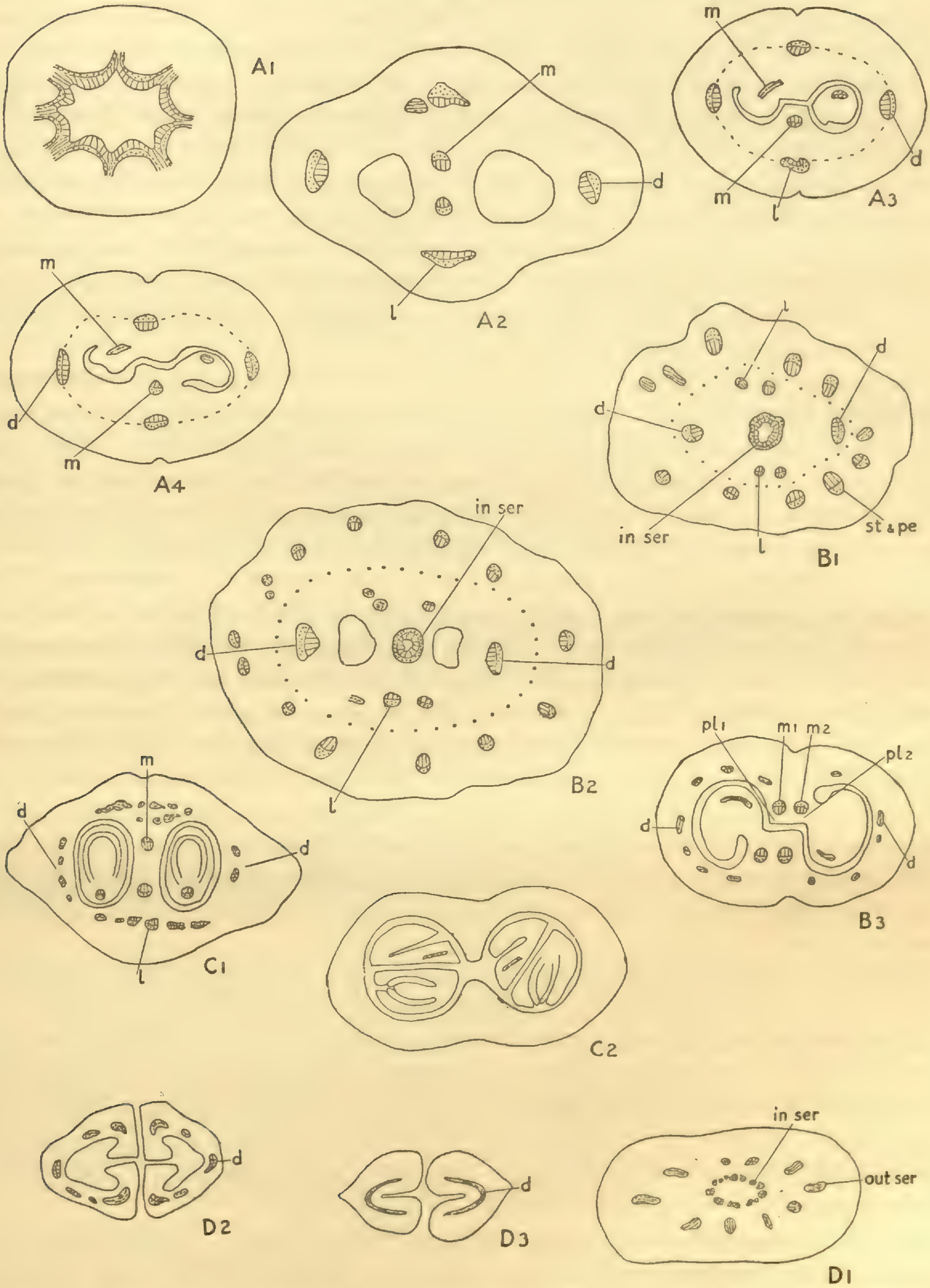
The development of the ovule of *Hamamelis virginiana* and *Liquidambar styraciflua* was described by Shoemaker ‡ in 1905, who found a nucellus of considerable bulk invested by two integuments and a parietal layer of cells similar to that formed in the nucellus of the Saxifragaceæ and Rosaceæ. The writer has examined the ovules of *Fothergilla*, *Corylopsis*, and *Parrotia*, and finds that they are constructed like those of *Hamamelis*.

Comparisons have been made from time to time by various writers between the genera of the Hamamelidaceæ and Cornaceæ that are provided with conspicuous involucral bracts. The writer has examined the bracts of *Parrotia*, and finds that they differ morphologically from those of the Cornaceæ. The bracts of *Parrotia* are tripartite, but this character cannot be easily observed, owing to the special development of one or other of the three segments. Since the foliage leaves and the lowermost bracts are stipulate, it appears that the coloured portion of the bract may correspond either to a stipule or the lamina of a leaf, and so differs from the bracts of the exstipulate genera, *Cornus* and *Davidia*.

The disposition and transformations of the stamens furnish other characters of interest from an evolutionary point of view. According to Baillon §, eight stamens are present in *Dicoryphe*, but the four alternipetalous ones are sterile, and again, in *Tetrathyrium subcordatum* and *Corylopsis*, glands occur in the interval between the stamens. Shoemaker ‖ points out that abortive pollen is sometimes developed in the nectaries present in the flowers of *Liquidambar styraciflua*, and he regards these

* E. Tanfani in Nuov. Giorn. Ital. vol. xxiii. (1891) 451–469, t. 4–7.
† H. Baillon, Histoire des Plantes, iii. 390 (*Hamamelis*); 391 (*Corylopsis*).
‡ D. N. Shoemaker, in Bot. Gaz. xxxix. (1905) 262.
§ H. Baillon, *l. c.* 392 (*Dicoryphe*); 391 (*Tetrathyrium*).
‖ D. N. Shoemaker, *l. c.* 262.

Text-fig. 1.



Diagrams illustrating the course of the floral vascular tissue in four genera of the Hamamelidaceæ:—
A 1, *Hamamelis arborea*; A 2–A 4, *H. Zuccariniana*; B 1–B 3, *Fothergilla major*; C 1, C 2, *Parrotia Jacquemontiana*; D 1–D 3, *Corylopsis spicata*. (Abbreviations, see p. 308.)

nectaries as reduced stamens. Oliver* states that the "didynamous squamæ" in *Eustigma* replace petals. An instance of the transformation of petals into stamens was observed by the writer in flowers of *Corylopsis spicata* gathered from Kew plants in 1909. The normal flowers possess five petals and five stamens. A complete transitional series occurred between the normal and the entirely apetalous flowers. The transitional flowers possessed foliose stamens, each consisting of a broad filament and rudimentary anther lobes. The genus *Fothergilla* possesses a number of stamens arranged in a single verticil. These emerge from a perigynous collar, which surrounds the ovary. The writer finds from seventeen to twenty-two in *F. Gardeni* and *major*. Baillon† investigated the development of the stamens and found that they represent several distinct whorls. Since *Fothergilla* is apetalous, it is possible that the outer whorls are really transformed sepals and petals.

The course of the vascular tissue has been followed in four genera:—*Hamamelis*, *Fothergilla*, *Corylopsis*, and *Parrotia*. The vascular cylinder (Text-fig. 1, A 1) separates, at the base of the ovary, into an outer and an inner series of bundles (D 1). The bundles of the outer series branch just below the level of the insertion of the perigynous ridge of tissue, to form externally the stemonal and perianth traces, *st* and *pe*; and internally the dorsal and lateral carpellary bundles, *d* and *l* (B 1, B 2). The former then leave the ovary. The inner bundles vary in number and disposition in different genera. In *Fothergilla*, two bundles are present in the septum as shown in C 1 (*Parrotia*), and each divides before leaving it to form two, which traverse the corresponding placentæ, B 3. Thus the bundle *m* (C 1) forms *m* 1 and *m* 2, which traverse *pl* 1 and *pl* 2 respectively (B 3). A single branch from *m* 1 supplies an ovule in the left-hand loculus and one from *m* 2 an ovule in the right-hand loculus. But in *Hamamelis Zuccariniana*, where the loculi are uniovulate, only one placenta corresponding to *pl* 1 and *pl* 2 is found, and the septal bundles, *m*, pass into it unbranched (A 3, A 4). In this case, one branch passes to the ovule from the bundle, *m*.

The above-described system is of a similar type to that which is found in the genus *Saxifraga*. It resembles in some details that of *Carpinus betulus*, described by Benson‡ and Welsford.

Summary.

1. A complete series from hypogynous to epigynous forms of flower exists in the Hamamelidaceæ, ranging from *Distylium*, by way of the perigynous genera *Hamamelis*, *Corylopsis*, and *Trichocladus* to *Eustigma*. Another series ranging from a *Distylium*-like form is only represented by *Sycopsis*, a genus which simulates epigyny owing to the fact that the ovary is invested by a closely adpressed perigynous tube. *Loropetalum* is epigynous, but the origin of this condition needs investigation.

2. The genus *Rhodoleia*, according to published descriptions, exhibits variability in the internal structure of the ovary.

* D. Oliver in Trans. Linn. Soc., Bot. xxiii. (1860) 83.

† H. Baillon in Adansonia, x. (1871) 127.

‡ Benson and Welsford in Ann. of Bot. xxiii. (1909) 630.

3. The ovules in *Hamamelis*, *Fothergilla*, *Corylopsis*, and *Parrotia* are suspended from *parietal placentæ* that are situated immediately above the septum in each.

4. The Hamamelidaceæ exhibit a complete series in the reduction of the number of ovules, ranging from *Liquidambar*, with numerous ovules in each loculus, by way of *Disanthus*, in which Baillon records three ovules in each series, and *Fothergilla*, *Corylopsis*, and *Parrotia*, with two ovules (one abortive) in each loculus, as in several Araliaceæ and Umbelliferæ, to *Hamamelis*, in which each loculus is uniovulate.

5. According to Baillon, the ovaries of *Hamamelis* and *Corylopsis* are often arrested in development and remain small and sterile. This feature is of special interest, owing to the fact that genera with polygamous and with unisexual flowers are frequent in the Hamamelidaceæ.

6. The ovules of the Hamamelidaceæ possess a bulky nucellus which becomes invested by two integuments and resembles in structure that of the Saxifragaceæ and Rosaceæ.

7. The bracts of *Parrotia* are tripartite and correspond morphologically to a stipulate leaf. One or other of the segments becomes specially developed and conspicuous. Hence the conspicuous portion may be homologous with either a stipule or the lamina of a leaf.

8. A complete series in the metamorphosis of petals into stamens has been observed in *Corylopsis spicata*.

9. The course of the vascular tissue in the flower has been followed in four genera—*Hamamelis*, *Fothergilla*, *Corylopsis*, and *Parrotia*. The same type prevails in them all and is similar to that which is found in *Saxifraga*.

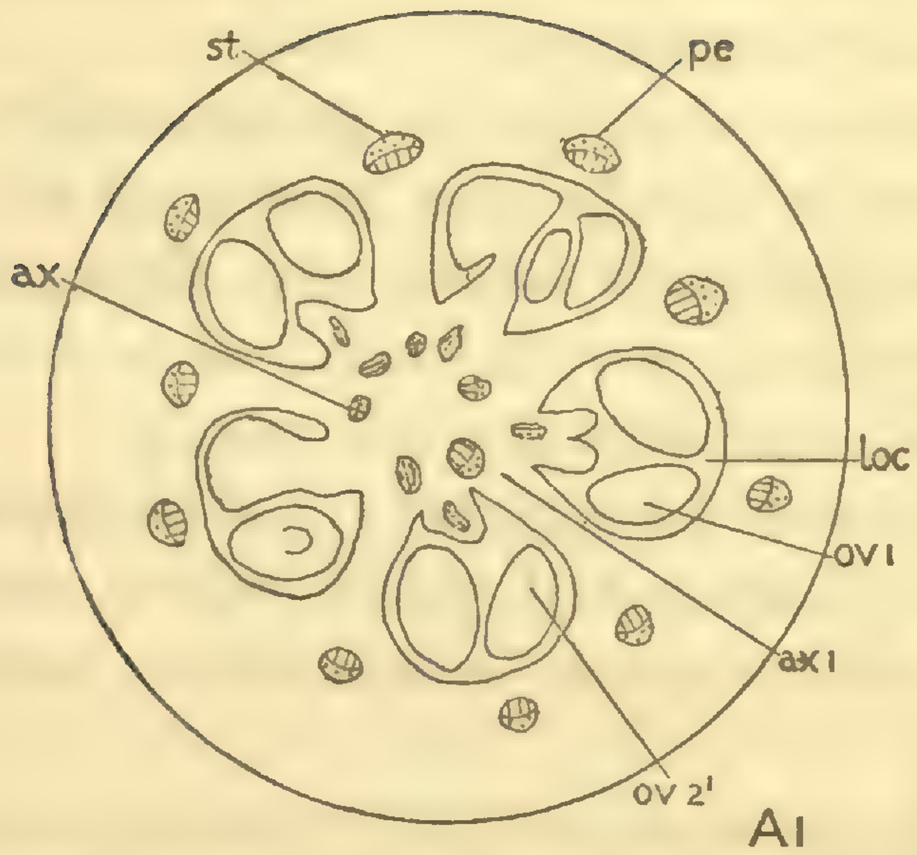
3. CAPRIFOLIACEÆ.

The general details of floral organization in the Caprifoliaceæ are so well known that they need not be recapitulated. Hence the morphology and vascular structure of the ovary and ovule will receive special consideration.

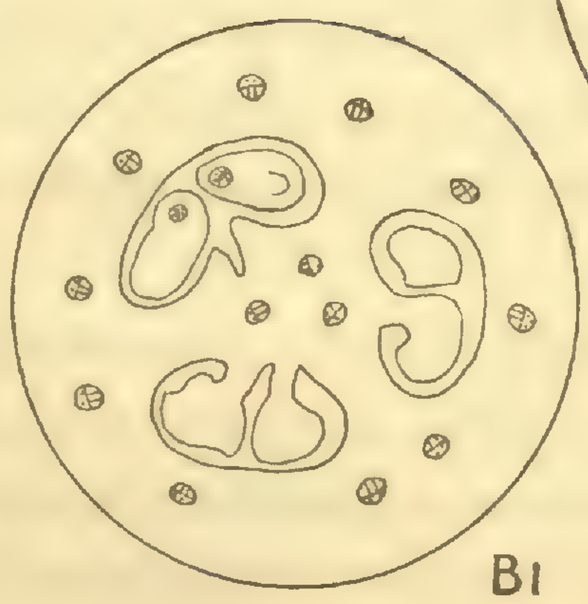
Morphology of the Ovary.

The ovary of *Leycesteria*, the type genus of the family, is five-chambered below, owing to the fact that the margins of the carpels are in this region congenitally united, forming a solid axial portion with radiating septa (Text-fig. 2, A 1), but the margins are free above, so that the accretion is incomplete (A 2). Hence the biseriate ovules are axially or parietally borne according to their situation. The fruit contains many seeds. *Lonicera* possesses a trilocular ovary, which is structurally similar to that of *Leycesteria* (B 1–B 3), but although the ovary is pluriovulate, few seeds are formed. Frequently in *L. Caprifolium* only one seed reaches maturity, the septa being ruptured or pushed aside by the developing seed, which eventually occupies the whole cavity of the ovary. Here the ovary does not undergo structural modification during growth in connection with the habit of producing few seeds. *Abelia* and *Linnæa* also possess trilocular ovaries of the *Leycesteria* type, but in each case one loculus is uniovulate, the ovule being

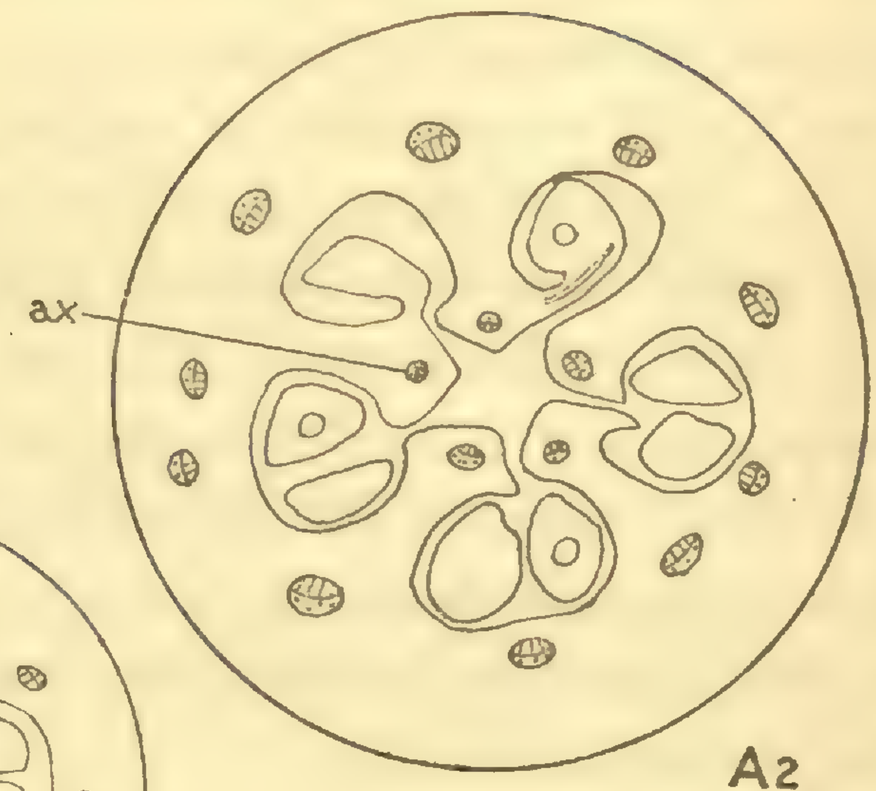
Text-fig. 2.



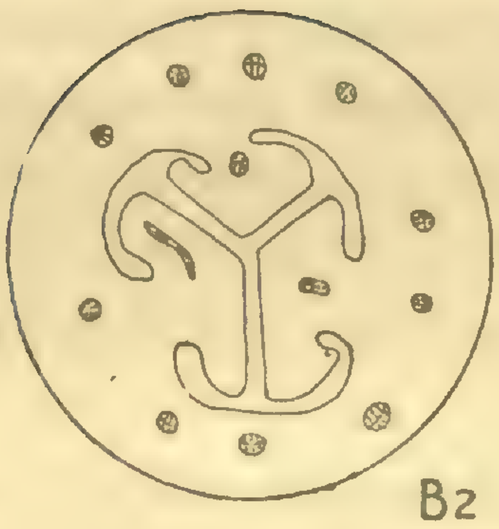
A1



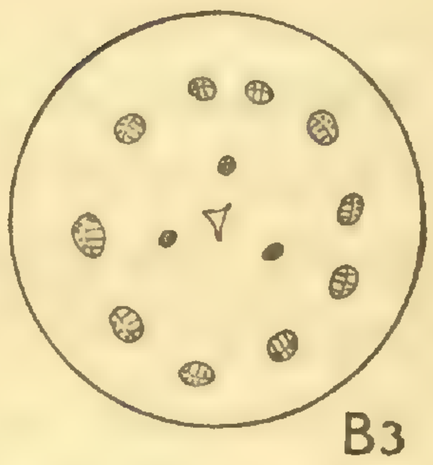
B1



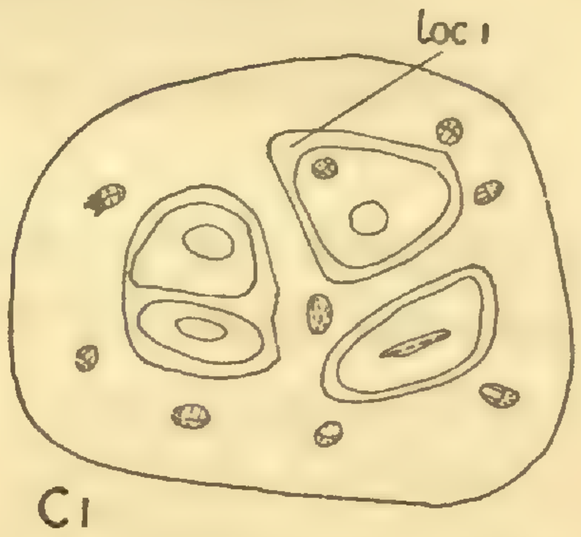
A2



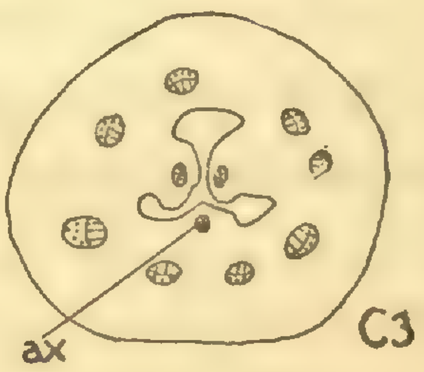
B2



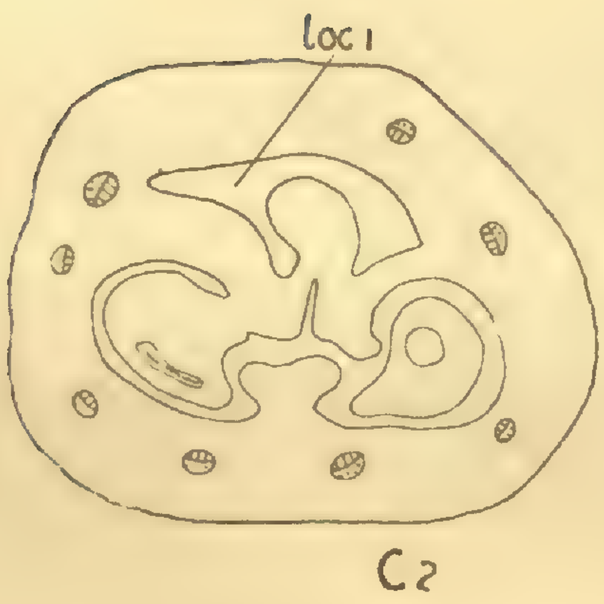
B3



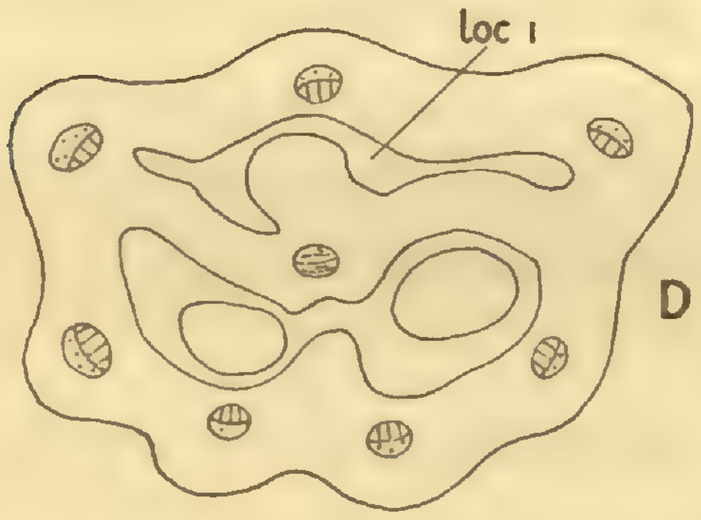
C1



C3

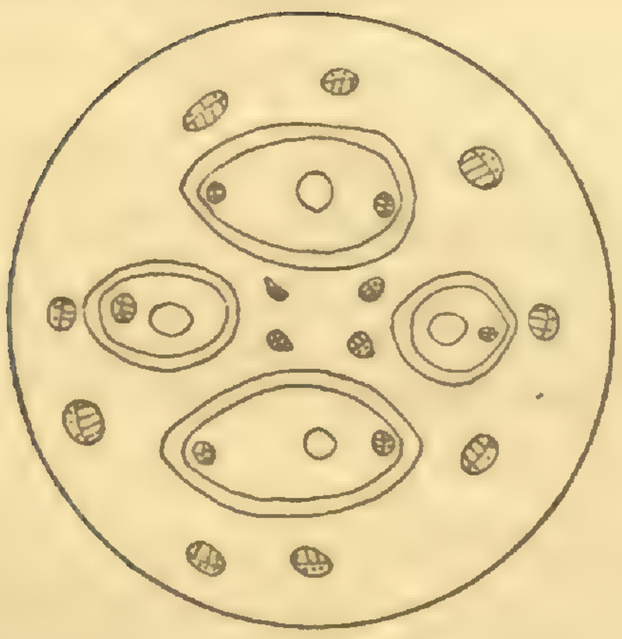


C2

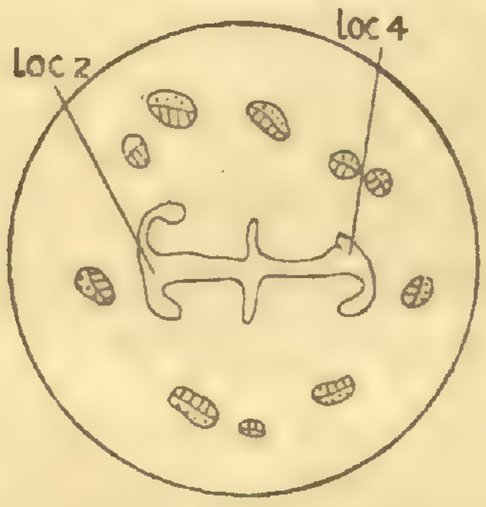


D

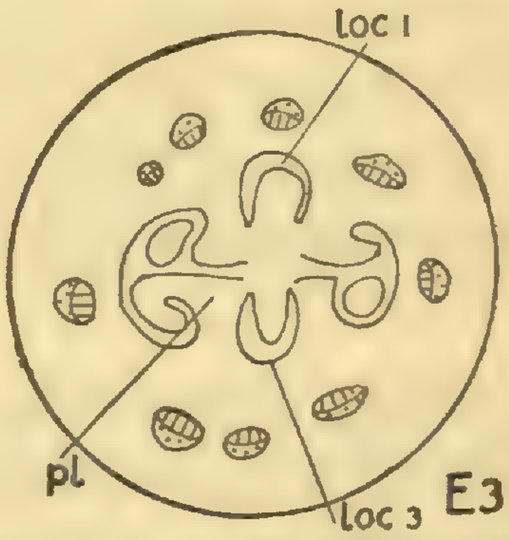
E2



E1



E4



E3

Diagrams illustrating the course of the floral vascular tissue and the arrangements of the ovules in Caprifoliaceæ :— A 1, 2, *Leycesteria formosa*; B 1–B 3, *Lonicera Periclymenum*; C 1–C 3, *Linnæa borealis*, *D. Abelia*; E 1–E 4, *Symphoricarpus racemosus* (continued in text-fig. 3).

suspended axially (D, C 1–C 3; *loc* 1). The structural agreement in this respect between *Abelia* and *Linnæa* is so close that it is impossible to distinguish between them. The genus *Dipelta*, established by Maximowicz *, possesses an ovary with two pluriovulate and two uniovulate compartments. Seeds are not formed in the pluriovulate loculi.

Symphoricarpus forms the next member of a remarkable series in which that portion of the ovary corresponding to the superior half in *Leycesteria* fails to develop. The adult flowers of *S. racemosus* are four-chambered below (E 1–E 3), but two-chambered in the very small upper portion, owing to the fact that the upper portion of the lateral carpel is incompletely developed (E 4; *loc* 2, *loc* 4). Each lateral chamber, *loc* 1, *loc* 3, contains a single axially suspended ovule. The loculi at right angles to these are pluriovulate, and the ovules which they contain are arranged in biseriate rows, suspended from the small adpressed parietal placentæ (E 3, *pl*) present in the upper portion of the ovary, with the exception of the lowermost ovule, which is axially borne. Only a single specimen of an entirely pentamerous flower was found; in this case the inferior portion of the ovary was five-chambered and the additional loculus uniovulate.

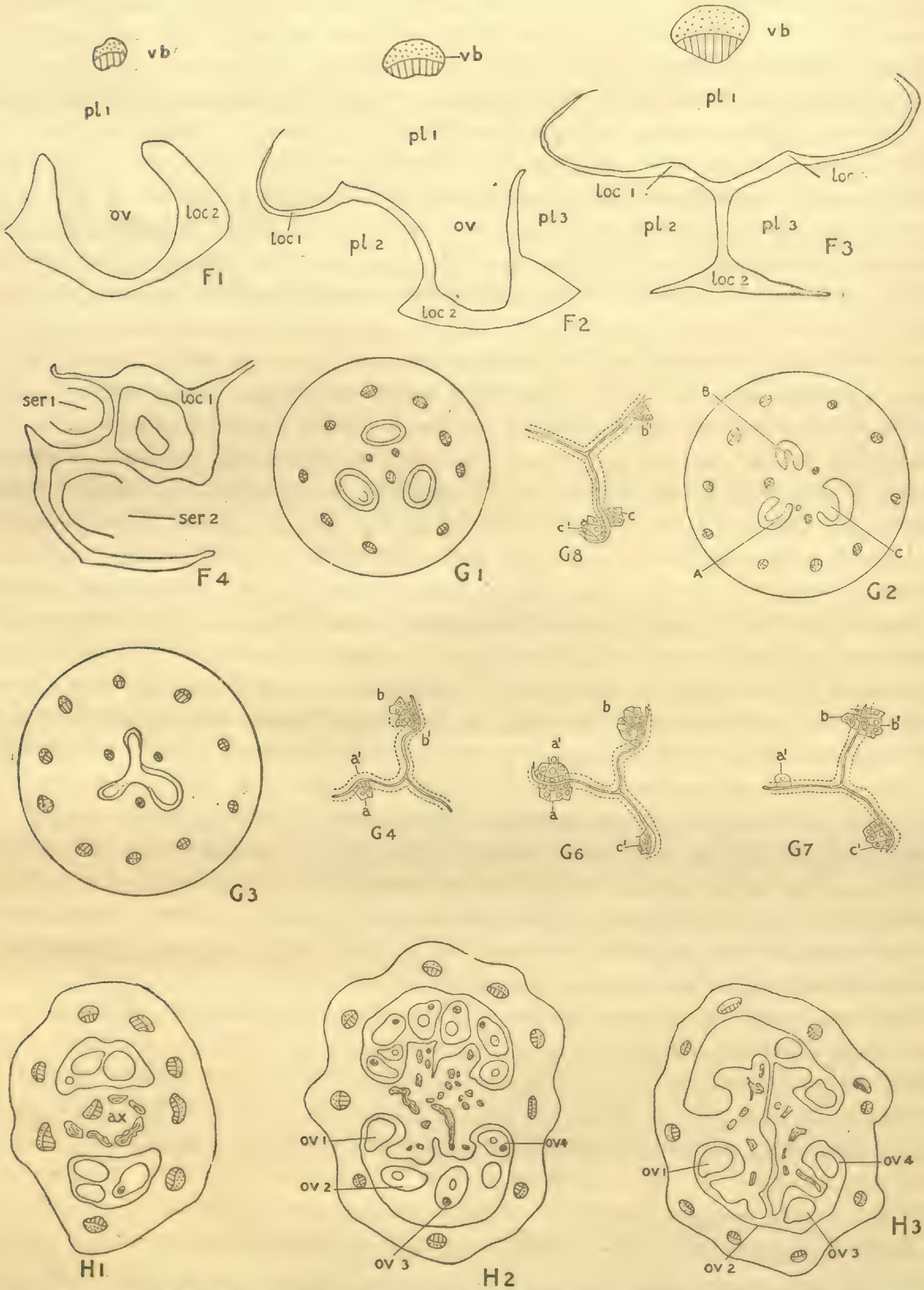
Abortion in the parietal portion of the ovary is carried still further in *Viburnum*, where, if the very young flowers of *V. Lantana* be examined, three united pairs of parietal placentæ may be observed (Text-fig. 3, F 2, F 3; *pl* 1, 2, 3). These are almost in contact with one another, so that they separate three compartments (*loc* 1, 2, 3). During subsequent growth only a single loculus (F 1–F 3; *loc* 2) develops as indicated in Text-fig. 4, leaving two upper arrested compartments (*loc* 1, 3). The latter are pluriovulate as previously recorded by Vidal †, and the ovules in each are arranged in two or more series (Text-fig. 3, F 4; *ser* 1, *ser* 2). At the same time Vidal, who made a special study of the development of the ovary in the Caprifoliaceæ, entirely overlooked the fact that the fertile ovule (F 1, *ov*) does not extend as it normally should do into either of the adjacent compartments (F 1–F 3; *loc* 1, 3), but into the loculus which has developed from the originally opposite compartment (F 1–F 3; *loc* 2). Again, the placentæ (*pl* 2, *pl* 3) do not bear ovules as they normally should do on the sides adjacent to *loc* 2. Finally, the fertile ovule does not actually form a member of the series of sterile ovules that arise from *pl* 1 and extend in *loc* 1 and 3. These features furnish an important clue to the interpretation of the peculiar morphology of *Viburnum*, which will be discussed after the vascular system has been described.

Sambucus forms the extreme member of the series under discussion. The number of loculi in *S. nigra* varies from two to five, but there are usually three. A single terminal axially situated ovule occurs in each loculus (G 2). The area above the ovules, which appears to form a part of the lower tissue region of the style, is in reality an exceedingly rudimentary parietal portion of the ovary, wherein the ovules are reduced to tiny swellings, arranged in short biseriate rows above the normal ovules. Figs. G 4–G 8 show the ovular rudiments arranged in the series *a*, *a'*; *b*, *b'*; and *c*, *c'* above the ovules A, B, and C, respectively (G 2). Hence it appears that the terminal ovules of *Sambucus*

* Maximowicz in Bull. Acad. Imp. Sci. Saint Pétersbourg, xxiv. (1878) 50.

† Vidal in Bull. Soc. de Statistique, Grenoble, 4 sér. t. iv. (1899) 157.

Text-fig. 3.



Floral structure in F 1–F 4, *Viburnum Lantana*; G 1–G 3, *Sambucus nigra*; G 4–G 8, the same, biseriate ovular rudiments; H 1–H 3, *Diervilla Lonicera*. (Abbreviations, see p. 308.)

occupy in the ovary an equivalent morphological position to those of the pluriovulate loculi in *Symphoricarpus*.

In *Diervilla* the portion of the ovary corresponding to the parietal region in *Leycesteria* is specially developed, the axial portion (H 1) being relatively small. Hence the greater number of the ovules are parietally borne. The opposite placentæ are in close contact, so that the ovary is rendered bilocular (H 3). In *Diervilla Lonicera* the ovules in each loculus are multiseriate (H 2, H 3, *ov* 1, 2, 3, 4), but in other species this arrangement is less definite. *Diervilla*, in the adpressed placentæ and multiseriate ovules, differs from all other Caprifoliaceæ.

The Ovule.

Hooker and Thomson * describe the ovule of *Viburnum Tinus* as consisting in its early stages "of a minute curved nucleus encircled with an annulus which is the only integument." This description applies equally well to the Caprifoliaceæ considered in this paper. The nucellus develops more or less obliquely, and is of comparatively small bulk. At maturity the ovules tend to occupy a tangential position in the loculus—that is to say, the nucellus and the vascular bundle of the raphe rest in a plane at right angles to a radial plane. They are not displaced from this position owing to abortion, but in *Symphoricarpus* the lowermost ovule of each biseriate row may be radially situated with the raphe abaxial, not adaxial as in the Araliaceæ.

Vesque in 1878 and Guignard in 1882 record that in *Lonicera* the embryo-sac is produced from a linear row of three cells. The writer finds that the single megaspore-mother-cell in the sterile ovules of *Symphoricarpus*, which are morphologically similar to the fertile ovules, produces not a linear row but a group of megaspores (Pl. 29. figs. 51–54, *m.sp*). Complete embryo-sacs were not observed in the sterile ovules. This suggests that the sterile ovules in *Viburnum* have become structurally modified in consequence of the loss of fertility, and that the raphe, the integument, and the nucellus have become degenerate. The megaspores of the normal ovule of *V. Lantana* are arranged in a linear row, as described by Hofmeister in his memoir of 1858; but the sporogenous tissue of the imperfect ovules originates from one or more subepidermal cells, of which each may produce a group of four cells (Pl. 29. figs. 55–57). Each megaspore, as a result of germination, produces an even number of nuclei, usually four or eight; but it is often difficult to trace them to their respective "megaspores," since the nuclei, from eight to sixteen and even more in number, appear to be situated in a single mass of protoplasm (Pl. 29. figs. 58–60). The energids resulting from the division of the "megaspores" do not become specially modified as in normal embryo-sacs. At the time when the perfect ovule has reached maturity, the energids are grouped to form hollow protoplasmic sacs which subsequently disintegrate.

Progressive reduction reaches an extreme in *Sambucus*. The tissue swellings, which correspond in situation to biseriate rows of ovules as shown in Text-fig. 3, G 4–G 8, are caused by the radial elongation beyond the normal of a small plate of sub-epidermal cells

* Hooker and Thomson, in "Præcursores ad Floram Indicam" (1855), Journ. Linn. Soc., Bot. ii. (1858) 163.

(Pl. 29. fig. 62). At the time of megaspore formation in the ovule each cell of the plate is filled with a finely reticulate cytoplasm and contains a resting nucleus. The nucleus subsequently divides to form two or four daughter nuclei, which are evident during the early stages of endosperm formation in the young seed, but soon disintegrate (Pl. 29. figs. 63, 64).

Course of the Vascular Tissue.

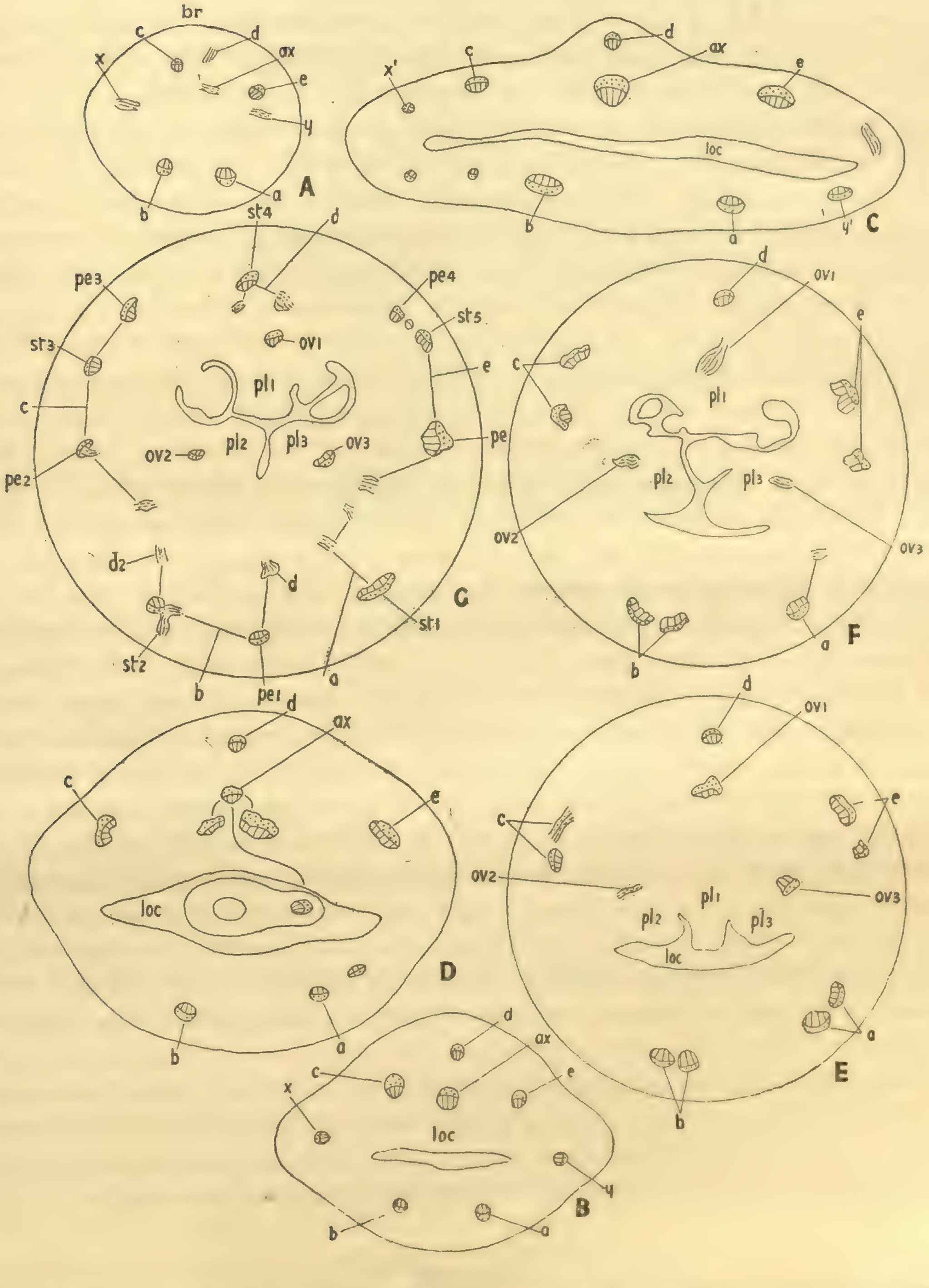
The vascular structure of the flower-stalk of *Leycesteria formosa* separates into an inner or axial (Text-fig. 2, A 1) and an outer or peripheral series of bundles. The bundles of the outer series extend upward in the wall of the ovary—those alternating with the loculi toward the stamens (*st*), those opposite the loculi toward the petals (*pe*)—and emerge from the terminal neck-like portion into the stamens and petals without entering into connection with the axial vascular strands. The presence of a single peripheral series of bundles is a feature which is constant for all the Caprifoliaceæ—in *Aralia* two distinct peripheral series are present, an outer relating to the perianth and stamens, and an inner composed of the dorsal and lateral carpellary bundles. But the number of bundles in the series is not constant: there are ten in *Leycesteria*, being equal to the sum of the petals and stamens; but in *Linnæa* (C 1) and *Diervilla* (Text-fig. 3, H) they are less than the sum, and only one-half the sum in *Viburnum* (Text-fig. 4, B, *a*, *b*, *c*, *d*, *e*).

The inner axial bundles are numerically equal to and alternate with the loculi in *Leycesteria*. They extend axially upward into the parietal placentæ (Text-fig. 2, A 2, *ax*) and finally into the style, where they alternate with the lobes of the stylar canal, as shown in C 3 (*Linnæa*). A similar grouping of the axial bundles obtains in the remaining genera. In *Lonicera*, where the ovary is trilocular, there are three axial bundles (B). In *Sambucus*, where the number of loculi varies from two to five, there is a corresponding variability in the bundles. In *Aralia* the absence of a loculus involves the absence of the corresponding axial and of the inner peripheral ovarian bundles, but in *Sambucus* only the axial bundles vary correspondingly.

Two ranks of ovules occur in each loculus of *Leycesteria*. It follows, therefore, that each axial bundle (such as, for instance, *ax* 1 in A 1) is adjacent to the rows of ovules (*ov* 1, *ov* 2′), the nearer series of each of the adjacent loculi, and receives corresponding series of vascular connections—one series from each row. Each ovule receives only a single bundle. A similar arrangement obtains in relation to the ovules in the pluriovulate loculi of *Symphoricarpus*, but the single ovule in each uniovulate loculus receives two connections, being in this respect the equivalent of a pair of ovules in the adjoining compartments. The vascular structure of the single ovule in *Sambucus* is similar to this.

Special attention has been given to the vascular structure of the flower of *Viburnum*, on account of its peculiar morphology. The floral vascular skeleton has been reconstructed from serial sections in a wax model (Pl. 30). This model will now be described, but the description should be followed with the aid of the diagrams of transverse sections

Text-fig. 4.



Diagrams illustrating the course of the vascular tissue in *Viburnum Lantana*. (Abbreviations, see p. 308.)

in Text-fig. 4. The position of the bracteole is marked *br*. Only five bundles, indicated by the letters *a*–*e*, extend throughout the ovary-wall. The bundles *a*, *b* are on the side opposite the bracteole, and the remainder on the side adjacent to it (A–D). The bundle *a* is connected with the stamen *st* 1; *b* with the petal *pe* 1 and stamen *st* 2; *c* with *pe* 2, *st* 3, and *pe* 3; *d* with *st* 4; and *e* with *pe* 4, *st* 5, and *pe* 5 (E, F, G). It is evident, therefore, that all the petals and stamens, with the exception of *st* 1, *pe* 1, and *st* 2, are connected with the bundles extending in one side of the ovary-wall—the side bearing the placentæ; so that a special enlargement of one part of the original wall—that opposite the placentæ—seems to have taken place. Besides the principal bundles, two smaller ones, *x* and *y* (B), are present, situated between *b* and *c* and *e* and *a* respectively. These die out upwards after branching and anastomosing with the adjacent principal bundles. Branches are shown at *x*′ and *y*′ (C). Figure G represents a transverse section of the model at the level *α*–*β* shown in Pl. **30.** It will be observed that small branches extend inward from the principal bundles just below the point of insertion of the stamens and petals—for instance, the branch *d* from *pe* 1 and *d* 2 from *st* 2. These branches represent the originally free dorsal and lateral carpellary bundles of the primitive flower. Similar branches occur in *Sambucus*, but they are entirely absent in *Leycesteria*, as mentioned above. Within the single series made up of principal and auxiliary bundles (*x*, *y*) there is another bundle, *ax* (A–D), which extends towards the placentæ and divides just below the ovule to form several small strands (D). Some of these collect to form the single ovular bundle. The remainder collect to form three strands, *ov* 1, *ov* 2, and *ov* 3, which extend upwards into the three placentæ, *pl* 1, *pl* 2, and *pl* 3 respectively (E). Thence they extend into the style, where they alternate with the above-mentioned dorsal branches. Hence it is clear that the bundle *ax*, owing to the extension of its branches into the placentæ, does not follow the course normally pursued by a peripheral bundle that relates specially to a parietally-borne ovule, but it is, on the contrary, analogous to the entire axial system of the Caprifoliaceæ with multilocular ovaries (Text-fig. 2). It is, therefore, not unreasonable to suppose that the bundle has been actually displaced from an axial to a peripheral position during the progressive abortion of the now rudimentary compartments. Assuming this to be the case, and taking also into consideration the morphological details already described relating to the ovule itself, together with the facts that rudimentary ovules are sometimes situated immediately above the fertile ovule and that rudimentary ovules do not arise from the placentæ (*pl* 2, *pl* 3) on the side of the fertile loculus, there is not the least doubt that the ovule now parietally situated was originally axially borne, but has suffered displacement concurrently with the displacement of the septa and axially extending vascular tissue. This solution of the morphology of the ovary brings *Viburnum* into line with the remaining Caprifoliaceæ.

Summary.

1. The Caprifoliaceæ show a complete series in the direction of abortion in that part of the ovary corresponding to the parietal portion in *Leycesteria*. The parietal region is rudimentary in the pluriovulate carpels of *Symphoricarpus* and in *Viburnum*. It is

extremely rudimentary in *Sambucus*, and obsolete in the uniovulate loculi of *Symphoricarpus*. The parietal region is also small in *Aralia* and the Hamamelidaceæ.

2. Progressive abortion in the ovary is associated with progressive sterilization. Physiological sterility occurs in *Lonicera* where although the loculi are pluriovulate, only a few seeds are formed in the ovary. The sterility of particular ovules is not pre-determined. In *Symphoricarpus* the ovules of the pluriovulate loculi, which are similar in form to the fertile ovules, are definitely sterile. The megaspores are not arranged in a linear row, as in the fertile ovule, and the embryo-sacs are incomplete. In *Viburnum* the sterile ovules are very imperfect. The integument and raphe are considerably reduced, and the sporogenous tissue develops abnormally. The ovules in *Sambucus* are represented only by a few cells. The Hamamelidaceæ also show stages in reduction in the number of ovules, but the stages are not similar in the two families.

3. The vascular structure of the flower exhibits a definite advance upon that of *Aralia* in the direction of economy. Instead of the double peripheral series of bundles which exists in *Aralia*, only a single series is present. By a further economical advance the peripheral bundles, which in *Leycesteria* are numerically equal to the sum of the petals and stamens, are reduced to one-half the number in *Viburnum*, arriving at a similar phase in the evolution of the vascular system of the flower to that attained by the Compositæ.

4. The Caprifoliaceæ mark an advance upon the typical Araliaceæ in the direction of progressive loss of carpellary autonomy. The styles are united, except in *Sambucus* and *Viburnum*. Again, the synthetic development of the vascular system has led to the disappearance in the body of the ovary of a distinct series of bundles corresponding to the inner peripheral series of dorsal and lateral carpellary bundles that exists in *Aralia*, *Acanthopanax*, and *Hedera*. This series is represented in the superior portion of the ovary of *Sambucus* and *Viburnum* by strands which connect the ovarian bundles with the stylar prolongations of the axial (marginal) bundles. But the connecting strands are absent in *Leycesteria* and *Lonicera*, so that the final traces of the dorsal bundles have disappeared.

5. The ovules of the Caprifoliaceæ are similar in structure, and take up a tangential position in the loculus. This position is unaffected by abortion. In *Symphoricarpus*, however, the lowermost sterile ovule in each pluriovulate loculus is radially situated, the raphe being abaxial.

6. The morphology of the terminal seed in the Caprifoliaceæ is rendered somewhat obscure, owing to abortion and sterilization in the ovary. The seed is axially suspended in *Sambucus*, and is in this respect analogous to the lowermost ovules in the pluriovulate loculi of *Symphoricarpus*. The seed, in *Viburnum*, has through abortion become displaced from the axial position which it originally occupied to a parietal position. Since rudimentary ovules occur immediately above the placental area of the seed, the latter also appears to correspond to the lowermost member of a series, as in *Sambucus*. The seed produced from the single ovule of the uniovulate loculus in *Symphoricarpus* may correspond to the lowermost ovule of the pluriovulate loculi; but, if so, the fact is not evident, since the parietal portion of the uniovulate carpels, perhaps owing to a sudden mutation, has

become entirely obsolete. It is clear that the terminal ovules of the Caprifoliaceæ have not all originated in the same manner, but they are either axially situated or of axial origin, whereas those of the Hamamelidaceæ and of *Aralia*, *Acanthopanax*, and *Hedera* are situated parietally.

7. The vascular structure of the single axially-suspended ovule in the genera with uniovulate loculi is similar to that of a pair of ovules in the pluriovulate loculi—two bundles enter the ovule and join to form one in the raphe. But in *Aralia*, *Acanthopanax*, and *Hedera*, and in the Hamamelidaceæ, where the terminal fertile ovule is parietally suspended, only a single bundle enters the ovule.

8. It is evident that the ovaries of several genera of Caprifoliaceæ have reached their present stage of construction in different ways, and in all probability from more than one prototype. *Leycesteria* and *Diervilla* present strong resemblances—both genera possess a tubular corolla with an irregular limb, the loculi of the ovary are in each case pluriovulate and the fruit polyspermous—nevertheless, the ovaries are structurally different. In *Diervilla* the placentæ are adpressed throughout the greater portion of the ovary; in *Leycesteria* they are congenitally united in the lower portion. Now, according to published descriptions, ovaries of both the above-mentioned types occur in the flower of the species of the Hamamelid, *Rhodoleia*. Hence it is not improbable that the structures obtaining in *Diervilla* and *Leycesteria* originated from prototypic ovaries fluctuating like those of *Rhodoleia* in the degree of centripetal development of the carpels. But it would be unwise to consider the prototypes necessarily identical, since the loculi in *Leycesteria* contain biseriate rows of ovules, whereas those of *Diervilla* may contain multiseriate rows. The latter condition recalls that of *Polyosma*, a genus included among the Saxifragaceæ in Engler's System.

The remaining Lonicereæ, with the exception of *Lonicera* itself and *Triosteum*, possess dimorphic carpels. *Abelia* and *Linnæa* differ in form and habit, but the ovaries are structurally similar; the same is the case with regard to *Symphoricarpus* and *Dipelta*. The ovaries of *Symphoricarpus* and *Triosteum* are structurally dissimilar, and must be regarded as having originated independently from an ovary constructed like that of *Leycesteria*.

The seriate rudimentary ovules of *Viburnum* and the biseriate rudiments present in *Sambucus* indicate that the ovaries in both genera were originally pluriovulate, whilst the structural characteristics of the ovary itself suggest that each has passed through the *Leycesteria* stage of construction. Nevertheless, the Sambuceæ have long been recognized as forming a distinct subsection of the Caprifoliaceæ, distinguished from the Lonicereæ, which possess congenitally united styles and a tubular corolla, by their rotate corolla and free styles. Indeed, Höck established a separate family for *Sambucus*—the Sambucaceæ. Moreover, from a study of the ovary in *Sambucus* and *Viburnum*, it seems clear that the process of abortion has been in each case a different one and dissimilar to the processes that have affected the construction of the ovary of the Lonicereæ. Hence the actual origin of the Sambuceæ remains obscure, and it is by no means certain whether the descent of either *Sambucus* or *Viburnum* could be legitimately traced to prototypic forms of the Lonicereæ.

4. CORNACEÆ.

Nine genera of Cornaceæ have been studied:—*Cornus*, *Marlea*, *Aucuba*, *Garrya*, *Helwingia*, *Corokia*, *Melanophylla*, *Griselinia*, and *Nyssa*.

Each genus is described separately, and the points are taken in the following order:—

Morphology of the flower and ovule.
Vascular structure.
Interpretations and comparisons.

(*a*) Cornus.

Morphology of the Flower and Ovule.

The genus *Cornus* was made the type of a new family, the Corneæ, by De Candolle *, and is characterized by possessing polypetalous, epigynous flowers with an inferior, bilocular ovary (rarely trilocular, according to Bentham and Hooker), surmounted by alternating tetramerous whorls of sepals, petals, and stamens. The genus *Benthamia*, established by Lindley † in 1833, which produces flowers of the *Cornus* type grouped to form a globular capitulum, is now regarded as a subgenus of *Cornus*, since the kind of inflorescence no longer forms a distinctive character.

The writer has devoted special attention to the following points:—Variability in the ovary, the structure of the style, the insertion of the ovules, and the structure of the nucellus.

The flowers of several species of *Cornus*, including *C. mas*, *C. sanguinea*, *C. Amomum*, *C. alba*, have been examined, but the ovaries have proved to be bilocular without exception. Benjamin Clarke ‡, however, records that he found several loculi in cultivated specimens of *C. sanguinea*. Thus he states:—"I have found, when cultivated in a nursery, the number of petals and stamens frequently increased to five, six, seven, or more—the greatest increase observed being eight petals and ten stamens, the ovary of the flower being four-celled; the carpels, however, sometimes increased to seven without any further increase of the petals and stamens."

The ovary of *Cornus*, which is terminated by a single style, might not be strictly bicarpellary, for several instances have been recorded in other families where the loculi and the styles present in the ovary belong to different carpels. Or, again, the style might be composed of the styles of four carpels. Now the structure of the style in *C. mas* does not afford a clue as to its composition. The stylar canal is ribbon-shaped and opens out eventually into the loculi. Clarke, however, observed important structural peculiarities in the styles of *C. alba* and *C. sanguinea*. He found that the canal in the upper part of the style is four-lobed—the lobes

* De Candolle, Prodromus, iv. 271.
† J. Lindley in Bot. Reg. t. 1579.
‡ B. Clarke in Hooker's Kew Journ. Bot. ii. (1850) 130.

alternating with the four-rayed stigma. This fact led to the expectation that either two or four units enter into the composition of the style. He then discovered that the lobes of the canal in *C. alba* and *C. sanguinea* are not orientated alike, being situated, in the latter species, opposite stamens instead of petals. In both species, the lobed canal passes into a ribbon-shaped canal, which is homologous with that in *C. mas*. Clarke's observations led him to the conclusion that the style is composed of the styles of two carpels, that two of the canal lobes are marginal and two sutural, and that the anomalous orientation in *C. sanguinea* is due to the imbricate disposition of the congenitally united styles. The writer's observations are in complete accord with those made by Clarke. Clarke also found in the case of a flower with a trilocular ovary that the number of canal lobes was increased by two—one marginal and one sutural—for each additional loculus.

The development of the ovary takes place in the manner described by Payer *—the projection is first of all flask-shaped; later, a basal ridge develops which divides the single cavity into two. The ovules arise from this ridge or septum, one on either side. The ovular mamelon grows downwards. During the downward growth the nucellus differentiates at the tip and is first directed towards the septum; later, it bends away from the septum, and turns obliquely upwards so that it assumes a tangential position. At the same time it is invested by a single integument.

The development of the ovular mamelon and differentiation of the nucellus were observed in *C. alba* and *sanguinea*. The structure of the young nucellus is shown in Pl. 29. fig. 67. Pl. 29. fig. 65 represents a vertical section through the ovule of *Benthamia*, in which the nucellus and an early stage in the growth of the single integument are evident. The nucellus resembles a sporangium, since the archesporial cells are much alike, but the sporangial appearance is partly due to viewing the nucellus in an oblique plane, for in fig. 66 (*Benthamia*) and fig. 67 (*C. sanguinea*) the cells are clearly arranged in rows and, in the latter case, one row (*ax*) is more noticeable than the rest. A complete series of preparations leading up to the fully-formed embryo-sac has not been obtained. The embryo-sac, however, appears to be formed in the normal manner from one cell of a row of four. A formation of parietal tissue has not been observed.

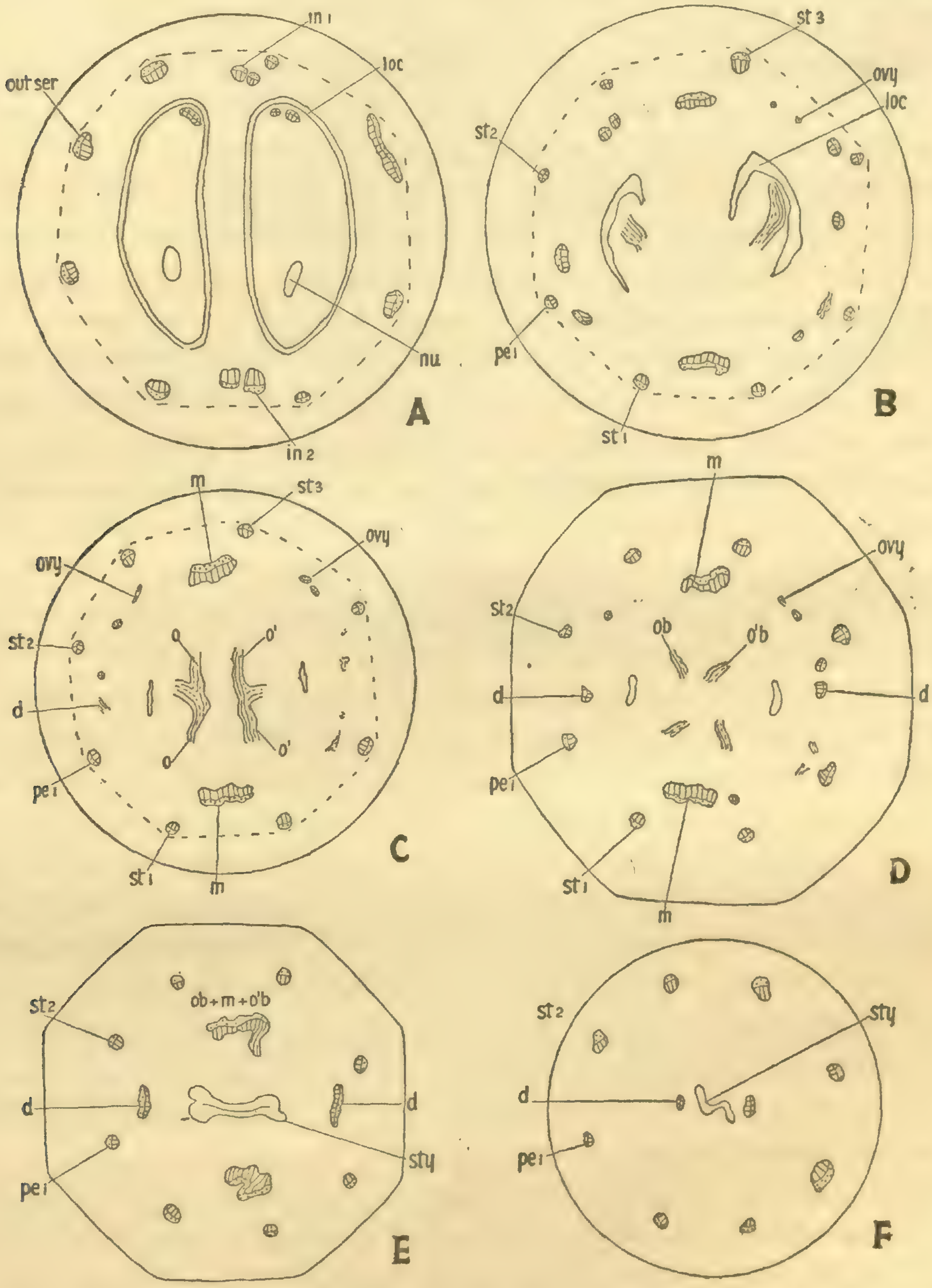
Vascular Structure.

The vascular tissue of the pedicel, in mature flowers of *C. sanguinea*, separates into an outer series (*out ser*) of eight and two inner bundles (*in*), all of which traverse the wall of the ovary (Text-fig. 5, A). Of the outer series, alternate bundles (*st*) extend towards the stamens and the remainder (*pe*) towards the petals B–F. Small inner branches, *ovy* (B, C), arise from the outer bundles before the latter emerge from the ovary—of which some unite to form the "dorsal" bundles, *d* (E, F), present in the style. The bundles *st* 1 and *st* 3 (A, B) opposite the inner bundles (*in*) do not branch.

* J. B. Payer, Traité d'organogénie comparée de la fleur (1854–1857), 418.

The inner bundles (*in* 1, *in* 2) are situated one at each end of the septum. Each divides into three (C, *o*, *m*, *o'*), the opposite lateral branches (*o*) unite and extend towards

Text-fig. 5.



Diagrams illustrating the course of the vascular tissue in *Cornus sanguinea*. (For abbreviations see p. 308.)

ovules on either side. The median branches (*m*) are joined by small branches; *o b* and *o' b* from *o* and *o'* respectively (D) pass into the style, one on each side of the canal (E), but soon die out, leaving only "dorsal" bundles present there (F).

Comparison with the Caprifoliaceæ and Hamamelidaceæ.

Kunth *, influenced by the resemblance between *Cornus* and *Viburnum*, placed the Corneæ, typified by *Cornus*, in the Caprifoliaceæ. But the Corneæ were soon afterwards separated from the latter to form a new family, the Corneæ (De Candolle †, Endlicher ‡) or Cornaceæ (Lindley §). Lindley considered that their habit and general characters, and especially their polypetaly, justified this removal. Bentham and Hooker note that the polypetalous condition is the only real distinctive character. It is, in the writer's opinion, a valuable one, for the Caprifoliaceæ are definitely gamopetalous, notwithstanding the fact that the corolla is highly variable in different genera.

In variance with Kunth, Lindley and Oliver ‖ are of opinion that the Corneæ more nearly approach the Hamamelidaceæ. Oliver considers even that the latter family may not improbably be regarded as a section of the former. Oliver is guided by general morphological resemblances, such as arrangement of the leaves, the form of inflorescence (capitate in *Benthamia* and *Nyssa capitata*), disposition of the stamens, the "inferior, bicarpellary and bilocular ovary," the ovules solitary and pendulous, etc. But the facts regarding the embryology of the Hamamelidaceæ revealed in Shoemaker's ¶ paper on *Hamamelis*, and those deduced from the study of the ovule in the Cornaceæ, are against the approximation of these families: in the Hamamelidaceæ, the nucellus is bulky, it is invested by two integuments and an extensive parietal tissue is formed, as in the Saxifragaceæ; whereas, in *Cornus*, the nucellus is small, without or with very little parietal tissue and invested by a single integument.

The writer finds a close correspondence in the floral organization between *Cornus* and the Sambuceæ, and *Cornus* and *Sambucus* may be profitably compared. The whorls in *S. canadensis* are pentamerous, those in *Cornus* tetramerous with the exception of the ovary. In both genera, the loculi are uniovulate, the ovules terminal, axially borne and tangentially orientated; the nucellus is very similar and invested by a single integument; with regard to the vascular structure, a single series of bundles is present in the ovary, dorsal branches pass into the style, and the vascular connections of the ovule are similar. Now the variability in the number of units contributing to the ovary in *Sambucus* is accompanied by a corresponding variability in the number of loculi, axial bundles, and styles, and the writer has expressed the opinion that the dorsal portions of the carpels have become definitely incorporated as an integral and invariable portion of the ovary-wall. Hence the ovary is not strictly bi-, tri-, or quadri-carpellary in bi-, tri-, or quadrilocular ovaries. Passing to *Cornus*, the presence of an additional unit, as shown by Clarke, is asserted by the appearance of an extra loculus, a peripheral ovular bundle and two additional lobes to the stylar canal, the structure of the ovary-wall remaining unchanged, as in *Sambucus*; so that it does not seem unreasonable to interpret the organization in terms of that of *Sambucus*, nor to consider the ovary bicarpellary

* Kunth, Nov. Gen. et Sp. iii. 430.
‡ S. Endlicher, Gen. Pl. (1836) 798.
‖ D. Oliver in Trans. Linn. Soc., Bot. xxiii. (1860) 83.
† A. de Candolle, Prodr. iv. 271.
§ J. Lindley, Veg. King. 2nd ed. (1847) 782.
¶ D. N. Shoemaker in Bot. Gaz. xxxix, (1905) 262.

by reduction from a quadricarpellary form, just as the ovary of *Sambucus nigra* may be considered bi-, tri-, or quadricarpellary by reduction from the symmetrical condition in *S. canadensis*. In the Hamamelidaceæ, the ovary is bicarpellary in the hypogynous state, and the bicarpellary condition is constant along the line of advance pursued by the flower in this family in the direction of epigyny.

If sympetaly does indeed constitute a real barrier between *Cornus* and the Sambuceæ, one is struck by the parallelism evident in the construction of the ovary, lessened only a little in importance by the occurrence of ovular rudiments and free styles in *Sambucus*.

(*b*) Marlea and Alangium.

Morphology of the Flower and Ovule.

The flowers of *Marlea* are hermaphrodite, and consist of an inferior ovary surmounted by isomerous whorls of from four to eight sepals, petals, and stamens—usually six, according to Clarke *, in *M. begonifolia*, seven in flowers of *M. platanifolia* growing at Kew, in 1910.

The flowers of *Alangium* resemble those of *Marlea*, except that the stamens may be equal to, or twice or four times as many as the petals. The ovary is unilocular.

The ovary of *Marlea*, according to Bentham and Hooker †, may contain from one to three loculi, or it may be unilocular in the upper and trilocular in the lower portion. Wangerin ‡ states that it consists of two carpels and may be either uni- or bilocular; he records a second smaller sterile loculus in *M. barbatum*. The writer has found only one-celled ovaries in *M. platanifolia*. Clarke § recorded an occasional increase in the number of carpels in *M. begonifolia* when growing under confined circumstances, "in one instance there were two additional imperfect cells separating the original cell and in another three fully formed fertile carpels." The ovary of *Marlea* terminates in a single style. The canal and the stigma are four-lobed in *M. begonifolia*, leading to the expectation that the style is made up of two or four units. Clarke compared the style with that of *Cornus alba* and interpreted it accordingly.

Bentham ‖ and Hooker state that the ovules are suspended from a central column in *Marlea*—that is, axially. Clarke's ¶ original figures of *M. begonifolia* confirm this statement.

The ovular mamelon, in the very young flower of *M. platanifolia*, almost entirely occupies the exceedingly small loculus. The mamelon grows downwards and the nucellus develops from it obliquely. The mature ovule is tangentially orientated in multilocular ovaries of *M. begonifolia*, from Clarke's ** figures. Harms and Wangerin

* B. Clarke in Hook. Kew Journ. Bot. ii. (1850) 131.
† Bentham et Hooker, Gen. Pl. i. pt. iii. 949.
‡ W. Wangerin in Das Pflanzenreich, 41 Heft, Alangiaceæ, 1.
‖ Bentham et Hooker, Gen. Pl. ii. 949.
** B. Clarke, *l. c.* pl. 5. A. figs. 8, 9.
§ B. Clarke, *l. c.* 130.
¶ B. Clarke, *l. c.* pl. 5. A. figs. 2, 8, 9.

state that two integuments are present and two are figured in 'Die Pflanzenfamilien' and 'Das Pflanzenreich' respectively. The writer has only observed the primordium

Text-fig. 6.

Diagrams showing the course of the vascular tissue in *Marlea platanifolia*. (For abbreviations see p. 308.)

of one integument, but the question cannot be definitely settled until slightly older flowers have been examined.

Vascular Structure.

The sections examined were obtained from very young flowers. The following description relates to the series through the oldest flower obtained prior to the upgrowth of the integument.

The toral vascular cylinder separates to form an outer series of fourteen bundles, which extend upward in the ovary-wall toward the petals and stamens (Text-fig. 6, A–G, *st* and *pe*), and an inner series of fine strands (B–E, *in ser*).

The bundles of the outer series branch before leaving the ovary to form series of inwardly extending strands (G, *ovy*). The latter behave in an irregular manner, but could not be traced into the style, and clearly correspond to the middle ring of bundles—equivalent to dorsal and lateral carpellary bundles—present in *Davidia*.

The bundles of the inner series are feebly differentiated, and extend as far as the point of insertion of the ovule (E, *in ser*): some originate directly from the toral cylinder (B, *in ser*), passing internally as far as the axis of the flower, then outward and upward in the ovary-wall; the rest arise from the outer bundles at a higher level (C, D).

The connection with the ovule could not be definitely settled. A small branch, *o*, could be traced from *ov* 1 (E), so that it is possible that branches from *ov* 1 and *ov* 2 unite to form the ovular bundle. Higher up in the series (F) the bundles *ov* 1 and *ov* 2 are still evident and *ov* 1 is present in the style (H). The remaining bundles of this series aggregate into two (F) which extend into the style (H). The bundles of the inner series are clearly concerned with supplying the ovule with nutriment, and appear to correspond with the innermost or septal bundles of *Davidia*. Clarke's * view of the bicarpellary condition of *Marlea* partly depended upon tracing the dorsal ribs of the carpels into the style, but it is now evident that the so-called dorsal ribs are merely collections of small ovular strands.

The axial extension of certain branches of the inner series at the base of the single loculus in *M. platanifolia* is curious, but *M. begonifolia* is often bilocular, and it is not improbable that the branches which are infralocular in *M. platanifolia* pursue a septal or axial course in bilocular forms of *M. begonifolia*.

Nature and Origin of the Flower.

The position of *Alangium* and *Marlea*, in the systems of different authorities, oscillates between the Combretaceæ and Cornaceæ. De Candolle †, who was followed by Lindley ‡, and for a time by Endlicher §, established these genera in a separate family, the Alangieæ, on the Combretacean side—an arrangement that, at the time, seemed consistent with the occurrence of multiseriate stamens and a unilocular ovary in both the Alangieæ and Combretaceæ.

* B. Clarke in Hook. Kew Journ. ii. (1850) 129.

‡ J. Lindley, Veg. King. 2nd ed. 719 (1847).

† A. P. De Candolle, Prodr. iii. 203.

§ S. Endlicher, Gen. Pl. 1184.

Baillon *, who was undoubtedly influenced by his researches † on the organogeny of the flower in the Amentiferæ, postulated a closer affinity. He had discovered that the ovary in *Quercus*, *Betula*, and *Castanea*, which is at first unilocular, becomes ultimately multilocular, owing to the slow inward or centripetal growth of the parietal placentæ, and compared the development of the ovary in *Castanea* with that in *Terminalia*, a genus of Combretaceæ. Moreover, Payer ‡, in describing the growth of the terminal placentæ in the latter family, had already demonstrated their parietal and centripetal nature. Baillon, accordingly and not unwisely, conceived the origin of the bilocular ovary in *Marlea* from the unilocular *Alangium*, supposing that the tendency towards centripetal development exhibited by the Combretaceæ had advanced further in *Alangium* and *Marlea*. He then inferred that a close affinity existed between the Combretaceæ and the Alangieæ, and literally swept the Alangieæ into the Combretaceæ.

Endlicher §, in 1847, discarded the idea of Combretacean affinity and transferred the Alangieæ to the Cornaceæ. Clarke ‖, in 1850, from his comparative study of *Marlea* and *Cornus*, advocated a very close affinity with the latter genus, stating that there is but little left to distinguish the Alangieæ and Cornaceæ. The view of Cornacean affinity held almost general acceptance until the advent of Wangerin's paper ¶; with this, the balance again inclines to the Combretaceæ. Engler at first accepted the opinions of Harms **, but later †† brings the Alangiaceæ into juxtaposition with the Nyssaceæ between the Rhizophoraceæ and Combretaceæ in the Myrtifloræ.

The facts accruing from this investigation do not, in the writer's opinion, favour one side more than the other. Baillon's hypothesis is plainly untenable for the following reasons:—Only one placenta is present in the ovary when unilocular, not two; the ovary-wall is much thicker on one side than on the other, leading to the expectation that a loculus has failed to develop; and, finally, the infra-locular vascular tissue, under the circumstances already discussed by the writer, suggests an originally axial or septal extension. The evidence, on the contrary, shows conclusively that the ovary is reduced.

Although *Marlea* agrees with *Cornus* in the placentation and orientation of the ovule, the resemblance between them is less close than Clarke supposed, and even the styles possess distinctive characters; the vascular systems, too, are dissimilar.

A thorough comparison cannot be made until the structure of the ovule and nucellus in *Marlea* is better understood.

* H. Baillon in Adansonia, xii. (Castaneacées), 1–20.
† H. Baillon in Adansonia, xi. (Corylées), 163.
‡ J. B. Payer, Traité d'organogénie comparée de la fleur (1854–1857).
§ S. Endlicher, Gen. Suppl. iv. part iii. 17 (1847).
‖ B. Clarke in Hook. Kew Journ. ii. (1850) 132.
¶ W. Wangerin in Das Pflanzenreich, 41 Heft, 6 (1910).
** Harms in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 8.
†† A. Engler, Syll. der Pfl. ed. VI. 179 (1909).

(*c*) Aucuba.

Morphology of the Flower and Ovule.

The plants are unisexual, and the bracteate flowers are borne in compound cymose racemes with branches arranged decussately. The female inflorescence bears a number of minute rudimentary, as well as perfect flowers. The male flower consists of alternating tetramerous whorls of sepals, petals, and stamens, the female of a unilocular ovary with alternating epigynous tetramerous whorls of sepals and petals. A few hermaphrodite flowers bearing two or three stamens were found on the female plants of *A. himalaica* growing at Kew in 1910. The ovary terminates in a style with an oblique stigma, which points towards the placental side of the ovary. Payer and Eichler state that the placenta is directed away from the bract; Baillon, that it may be directed away from the bract, towards it, or laterally; the writer finds that it may occupy any one of the four antepetalous or alternipetalous positions. Hence the orientation of the ovary relative to the perianth is variable. The development of the flower has been accurately described by Payer—its primordium resembles an incomplete circular ridge (this becomes circular with an oblique opening); as growth proceeds, the mamelon becomes ovoid enclosing a cavity—the loculus,—and the narrow orifice forms eventually the slit-shaped stylar canal. The placenta, which is terminal and bilobed in transverse sections of mature ovaries, arises as a well-defined bulge from the ovary-wall. The single descending ovule develops at the end of this protuberance. The ovaries are very rarely biovulate. One biovulate ovary was found in *A. japonica*—the additional ovule developed from a placenta on the opposite wall of the loculus, but the ovary remained unilocular; the stigma was unequally bilobed. Two out of twenty ovaries were biovulate in *A. himalaica*; the stigmas were irregularly lobed—perhaps an abnormal feature, since a capitate stigma is figured in Hooker's * illustrations of this species.

The earliest stages in the development of the ovule, prior to the differentiation of the nucellus, are shown, in vertical section, in Text-fig. 13, F, G. The pivot-cells at the point where the mamelon bends away from the ovary-wall are indicated at *p*. In G the portion of the mamelon below the pivot-cells shown in F has elongated considerably, owing to cell-division, and three regions of special merismatic activity are to be observed. The lowermost of these is localised at *un int*, which is the primordium of the lower rim of the integument; the next is confined to the primordium of the nucellus, *nu*; the third and uppermost, *up int*, extends from the upper edge of the nucellus to the pivot-cells on the adplacental side of the ovule. Here the cells are providing for horizontal extension. The next stage (D) shows the ovule after considerable growth has taken place; the chalazal region is now clearly defined and the nucellus has turned through an angle of 45°. This has been accomplished by the longitudinal elongation of the abplacental (*ab*) end of the ovule during chalazal differentiation, whilst the adplacental (*ad*) side has undergone less longitudinal, but

* J. D. Hooker, Illustr. Himal. Plants, 12.

more horizontal, extension. The under-margin of the integument has now enclosed and extended beyond the lower end of the nucellus, and its upper concave end forms the floor of the micropyle. The upper portion of the integument, which Baillon styles an obturator, is of considerable bulk and of an unusual type. It invests the upper surface of the nucellus and forms the roof of the micropyle. It consists of cells arranged in curved rows (*int r*), clearly shown in D, E, that have originated from the short rows shown in G. This curvature is due to the growth-changes, which cause the rotation of the nucellus. The nucellus is entirely free from the integument. Subsequent growth-changes place the axis of the nucellus towards the vertical, and are more concerned with the development of the lower portion of the ovule.

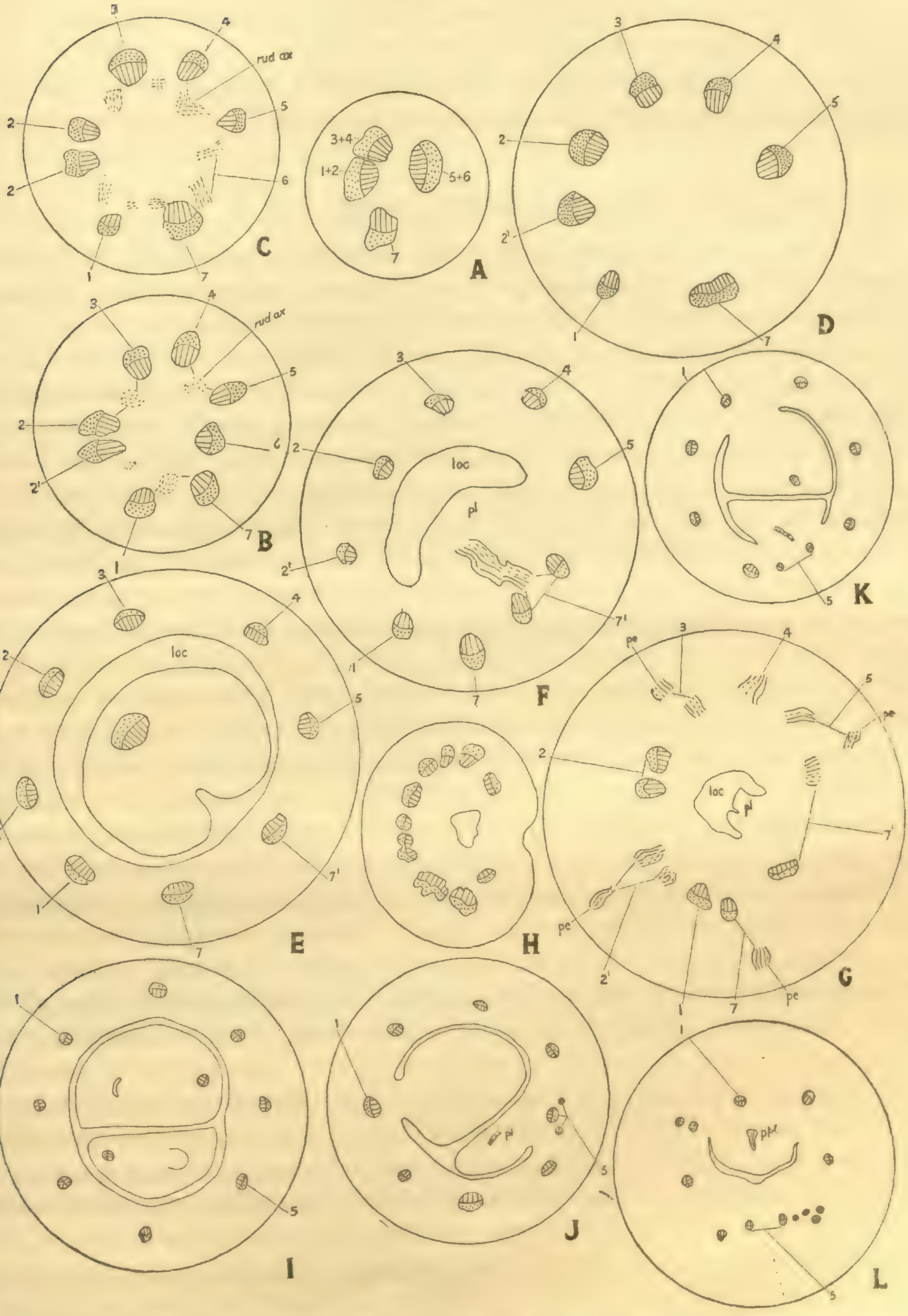
A complete series of stages in the development of the nucellus has been obtained. When the ovule has reached the stage shown in G, the nucellus already consists of several short axial rows of cells. From Pl. 29, fig. 69 it is evident that the primary archesporial cells have divided to form primary parietal and sporogenous cells. In one row further divisions have ensued, resulting in the formation of three parietal and two sporogenous cells. The next stage was obtained in *A. himalaica*, where a linear row of four megaspores and a definite layer of parietal tissue had been formed. The embryo-sac, in the case shown in fig. 70 (*A. japonica*), will evidently be formed from the lowermost member of the linear row, being relatively deep-seated. Sometimes more than one megaspore prepares to germinate, as in fig. 71 (*A. japonica*), megaspores of adjacent rows; and in fig. 72 (*A. himalaica*) a second megaspore is situated near the embryo-sac, which, in this case, appears to be the third cell of the row. During the formation of the megaspores, the nucellus increases in bulk by division of the cells forming the axial rows. The epidermal cells also undergo division (fig. 70). The embryo-sac develops in the normal manner.

Vascular Structure.

A reconstruction of the vascular system of the flower of *A. japonica* was made in wax from serial transverse sections of a particular flower. The vascular system of this flower will now be described, and can be best followed by diagrams of transverse sections (Text-fig. 7). Three bundles of different sizes are present in the pedicel (A): of these the largest (A, 1, 2, 3, 4) divides first to form two and ultimately five bundles (B, 1, 2′, 2, 3, 4); another (A, 5–6) divides once—one branch forms a principal bundle (B, 5), the other (B, 6) extends towards the axis a little and divides into two small branches (C), which extend outward again and join the principal bundles (C, 5, 7) on either side; the third (A, 7) forms two principal bundles (D, E, 7, 7′). Rudimentary axial branches are formed from the other bundles evident in the pedicel (B, C, *rud. ax.*)

The principal bundles extend as far as the point of insertion of the ovule without branching (F), and then each divides to form two or three smaller branches (G); four of these leave the ovary—one to each petal (G, *pe*),—the remainder form first an arc-shaped group (H) and higher up a single bundle in the style.

Text-fig. 7.



Diagrams showing the course of the vascular tissue in the female flower of *Aucuba*; A–H, uniovulate ovary; I–L, biovulate ovary. (For abbreviations see p. 308.)

The ovular bundle is directly connected with a principal bundle; and the latter divides into three, of which the median extends into the ovule (F). In another flower, branches from the adjacent principal bundles unite to form the ovular bundle.

The diagrams I, J, K, L are drawn from sections of a biovulate ovary. The ovular bundles originate from the principal bundles 1 and 5 (I, J).

The Nature and Origin of the Flower.

Aucuba was first of all placed among the "genera Corneis affinia" of Endlicher's System *, but later included among the Corneæ †, under a subfamily, the Aucubeæ. It has remained closely associated with *Cornus* in subsequent systems.

Diverse interpretations have been made of the nature and origin of the unilocular ovary. Baillon ‡ argued the probable derivation of the ovary of *Cornus* (bilocular) from that of *Aucuba* by the centripetal ingrowth of parietal placentæ, pointing out that the ovary of *Garrya* formed a connecting-link between the two. This argument would imply that the ovary is polymerous, consisting of carpels united by their margins.

According to Eichler §, on the other hand, the ovary is monomerous. Wangerin ‖ considers it to be monomerous by reduction:—"Der underständige Fruchtknoten wird hier von einen einzigen Karpellblatt gebildet" and "*Cornus* bildet das Zentrum dieser Gruppe, von dem sich *Aucuba* hinsichtlich der Reduktion in Gynæciums am weitesten entfernt."

Now the ovary of *Aucuba* could be easily synthesized from carpels which become united by their margins, and, if this were so, Baillon's hypothesis would carry weight, since the carpels retain the potentiality for centripetal ingrowth. But the vascular evidence at present turns the scale in favour of a different explanation. The rudimentary branches at the base of the loculus recall the similarly situated infra-locular branches in *Marlea platanifolia*. It was suggested in this case that the infra-locular branches extend as axial or septal bundles in septate forms of *Marlea begonifolia*. Hence, in the case of *Aucuba*, it seems not unreasonable to suppose that the curious infra-locular rudiments represent an axial or septal system that existed in the primitive flower. If this were so, the ovary was probably quadrilocular and hence tetramerous. The primitive ovary of *Aucuba* may be likened to that of *Viburnum*, the effect brought about by abortion, however, being different in the two cases. It was deduced for *Viburnum*, from the peculiar floral morphology and vascular structure, that the parietally placed ovule was originally axially suspended—the abortion of septa being evidently accompanied by the displacement of the axially borne ovule and axial vascular tissue to a peripheral position. But anomalies of the kind described for *Viburnum* do not occur in *Aucuba*, so we may conjecture that the axially suspended ovules present in the primitive *Aucuba* disappeared with the septa, leaving only a single parietally borne ovule in the ovary. In

* S. Endlicher, Gen. Pl. 798.
† S. Endlicher, Gen. Pl. Suppl. iv. part 3. 18.
‡ H. Baillon in Bull. Soc. Linn. Paris (1877) 139.
§ Eichler, Blütendiagr. ii. (1878) 415.
‖ W. Wangerin in Engl. Bot. Jahrb. xxxviii. Heft 2 (1906) 6, 50.

biovulate ovaries, the ovules from their situation belong to different carpels, but the manifestations of the second unit are confined to the additional ovule and a small additional stigmatic lobe. Here, again, as in *Sambucus*, the dorsal portions of the carpels have become a permanent portion of the ovary-wall and are non-variable. The entity of the carpel is almost completely lost, so that the disappearance of the septa must be regarded as only modifying the polymerous condition of the ovary; the ovary is not reduced to a single carpel.

The polymeric hypothesis outlined above receives contributory support from the evidence that has been deduced from studying the course taken by the vascular tissue in the flower. The principal bundles are clearly composite—that is to say, they exist or existed in relation to more than one organ, as they do, for instance, in *Viburnum*. Thus, in the upper part of the ovary, the bundles connected with the petals branch. These branches are comparable to the carpellary bundles, which traverse the style in *Sambucus* and *Cornus*; whilst the remaining alternate bundles occupy the site of stemonal bundles, although stamens are absent (when a stamen, normally present, is absent, as in *Aralia*, *Davidia*, and *Helwingia*, the corresponding bundle is absent also). Hence each of the eight bundles, in *Aucuba*, is partly of carpellary origin. If the carpellary element in each is alternately of "ventral" and "dorsal" origin, in correspondence with the bundles of *Garrya*, this would indicate a tetramerous ovary. But, on the other hand, the carpellary elements might have originated from a single carpel of the type found in *Davidia* and the Araliaceæ, having several bundles. The evidence afforded by biovulate ovaries, however, is opposed to the latter possibility, since the appearance of an additional unit is not accompanied by a corresponding increase in the number of carpellary branches in the style—an increase which, according to Benjamin Clarke, happens with the manifestation of an additional unit in *Cornus*.

If these speculations are correct, the flower was originally hermaphrodite and the ovary polymerous—multilocular in its lower, unilocular in its upper portion, as in *Leycesteria*. By analogy with the Caprifoliaceæ and Hamamelidaceæ, but perhaps prior to the attainment of epigyny, the loculi were pluriovulate—the ovules in the lower portion axially, those in the upper portion parietally borne. Then the septa disappeared and the ovules were numerically reduced, leaving only a single parietally suspended ovule analogous to the single fertile ovule present in the loculi of *Aralia* and *Hamamelis*.

Now it is evident, from the facts that have been enumerated for both *Cornus* and *Aucuba*, that considerable differences exist between them. First, the ovule of *Cornus* is suspended axially—a situation that is constant for the Caprifoliaceæ with terminal ovules; whereas, in *Aucuba*, it is borne upon a parietal placenta—a placentation apparently constant for the terminal ovules of the Hamamelidaceæ. This difference is one of fact, and does not depend upon the hypothesis of origin outlined above. Secondly, the nucellus in *Aucuba* exhibits distinctive characters, and in its primary bulk, definite "calotte" epidermal cap, and subsequent girth-extension, owing to cell-multiplication, is closely comparable to that of the Rosaceæ.

(*d*) Garrya.

Morphology of the Flower and Ovule.

The plants of *Garrya* are diœcious. Both the male and female inflorescences are catkin-like. The flowers are situated in the axils of decussate bracts, either singly as in *G. Fadyenii* and the majority of the species, or in groups of three as in *G. elliptica*. The bracts are free in *G. laurifolia*, free and foliaceous in *G. ovata*, but connate at their bases and foliaceous toward the lower end of the inflorescence in *G. Wrightii*.

The male flower of *G. elliptica* consists of an outer whorl of perianth leaves, an inner whorl of four stamens which alternate with the perianth divisions and centrally situated rudiments of an ovary. Payer *, who studied the development of the flower in *G. elliptica*, states that two whorls of perianth leaves are present :—"Le périanth est double et composé : l'externe d'un petit bourrelet à quatre dents dont deux sont latérales et un peu plus grande que les deux autres situées, l'une en avant et l'autre en arrière ; l'interne, de quatre divisions alternes libres entre elles jusqu'à la base." Similar observations were made by Baillon †, who also described the development of the flower in this species. Harms ‡ discovered a small tooth-like process alternating with the perianth divisions—also in *G. elliptica*,—which he identified as a rudimentary calyx leaf. But Wangerin §, from a study of several species, points out that the projections observed by Harms are homologous with bracts. The writer has not reinvestigated the development, but is unable to detect the presence of a second whorl in the mature flowers of *G. elliptica*.

Bentham and Hooker ‖, in 'Genera Plantarum,' and De Candolle, in 'Prodromus,' note that the stamens are opposite the calyx lobes in some species of *Garrya*. "Stamina calycis lobis in aliis speciebus alternata, in aliis certe opposita." The information is evidently derived from Bentham's ¶ description of the new Mexican species, *G. laurifolia* and *G. ovata*, in 'Plantæ Hartwegianæ' :—"Stamina in utraque specie laciniis perigonii opposita, sic etiam ut videtur *G. elliptica*." But no reference to opposite stamens occurs in Harms's diagnosis nor in Wangerin's monograph on the Cornaceæ. For this reason it became eminently desirable to settle the point definitely. Accordingly, Dr. Rendle very kindly allowed the writer to examine specimens of the male flowers of *G. laurifolia* (one of the species in question) from the Herbarium of the British Museum of Natural History. Two portions were dissected. Each consisted of a terminal flower and the lateral axillary flowers situated immediately below. In both specimens the uppermost bracts were small and resembled the perianth segments. Owing to this circumstance, one of the terminal flowers (Pl. 28. fig. 22) appeared to consist of an outer whorl of six perianth segments and an inner whorl of four stamens ; of the latter, two were opposite the perianth-like bracts (*br*). The other terminal flower (fig. 24) consisted

* J. B. Payer, 'Leçons sur les Familles naturelles des Plantes' (1860–1865) 124.

† H. Baillon in Bull. Soc. Linn. Paris, i. (1877) 139. ‡ Harms in Ber. Deutsch. Bot. Gesell. xv. (1897) 19.

§ W. Wangerin in Engl. Bot. Jahrb. xxxviii. Beibl. n. 86 (1906) 52–53.

‖ Bentham et Hooker, Gen. Pl. i. 951. ¶ G. Bentham, Plant. Hartwegianæ, 14.

of an outer whorl of five leaves and an inner of three single and one branched stamens (*st*), so that it simulated a pentamerous flower. One of the stamens (*st*) was situated opposite the bract. But the lateral flowers (fig. 25) of both specimens resembled those of *G. elliptica*—the stamens were alternate with the perianth segments. Bentham seems to have fallen into error through examining the terminal flowers of the inflorescence.

The male inflorescence of *G. Thuretii*, a hybrid between *G. elliptica* (male) and *G. Fadyenii* (female), called in error *G. Macfaydiana* by Carrière, discovered by M. Gustave Thuret at Antibes about 1862, combines the characters of both parents This point was overlooked by Carrière* in his descriptions published in the 'Revue Horticole,' of 1869 and 1879, and subsequently by Baillon†, who states that the male flowers resemble those of *G. elliptica*. The material upon which the following observations are founded was gathered at Kew from plants obtained from France about the year 1896. The "flowers" occur singly in the axil of each bract, agreeing thereby with the female parent, but each stalk bears in reality three, more or less congenitally-united flower-heads, so that there is a marked correspondence with the male parent. There were from four to six perianth leaves in the specimens examined, and in some cases two or three were congenitally united to form a lobed structure. The stamens varied in number from four to twelve: the outer were usually of normal size, the inner smaller and often rudimentary.

The female flower consists of a bicarpellary ovary terminated by two, almost free, styles and surmounted in *G. elliptica* by a pair of minute folioles, which are situated almost at right angles to the styles. Lindley‡ regarded the folioles as a calyx and they are described as such by Harms§ in 'Die Pflanzenfamilien.' Baillon‖, on the other hand, points out that the terminal flowers of the inflorescence often bear on the sides of the ovary near mid-height two bracts which alternate with the two preceding normally orientated ones; for this reason he considers that the supposed sepals are nothing more than displaced bracts. Wangerin¶ investigated the matter in greater detail, and his original figures show a complete series in the displacement of bracts, thus:—The folioles are absent in *G. gracilis* (Wang., fig. 5, D); they are situated at about one-third the height of the ovary in *G. Wrightii* (Wang., fig. 4, D); they are depicted higher up still in *G. laurifolia* (Wang., fig. 2, D), and terminal in *G. Fremontii* (Wang., fig. 2, C). Having examined herbarium specimens of several species of *Garrya*, notably *G. Veitchii* and *G. laurifolia*, the writer is able to confirm Wangerin's observations.

The development of the female flower of the hybrid, *G. Thuretii*, was described by Baillon** as follows:—"Sa fleur femelle est-elle representée au début par un mamelon plein qui occupe l'aiselle d'une bractée de l'inflorescence. Bientôt sur ce mamelon se montre, à droite et à gauche, une feuille carpellaire. Toutes deux s'elèvent en devenant connées et constituent la cavité de l'ovaire, que leurs sommets couronnent ensuite en

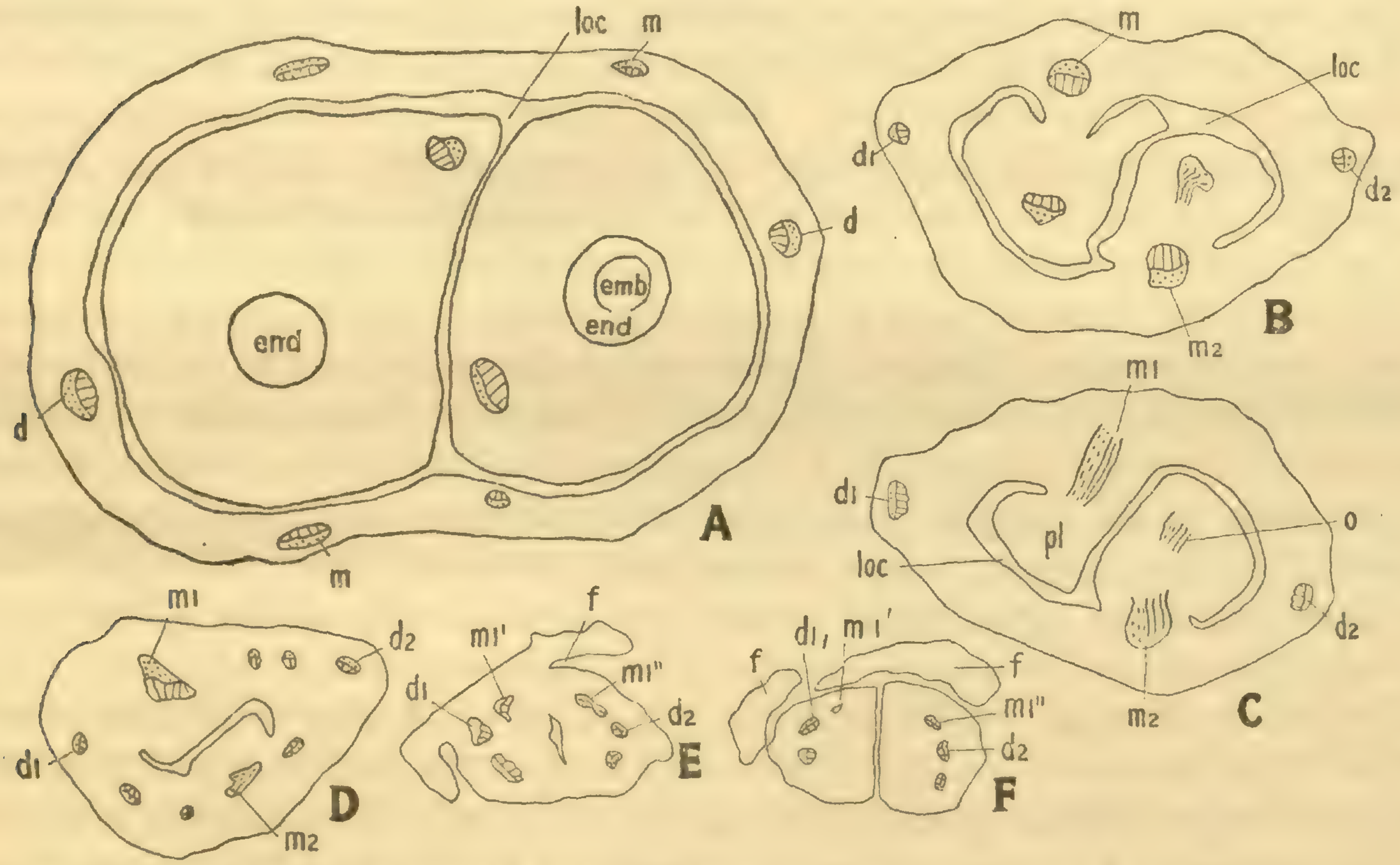
* E. A. Carrière in Revue Hort. 1869, 17, and 1879, 154.
† H. Baillon in Bull. Soc. Linn. Paris, i. (1877) 139.
‡ J. Lindley, Veg. King. 2nd ed. 295 (1847).
§ Harms in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 8, 256.
¶ W. Wangerin in Das Pflanzenr. Heft 41 (1910), Garryaceæ, 1–17.
‖ H. Baillon, *l.c.*
** H. Baillon, *l.c.* 140.

divergeant de deux branches stylaires latérales." The parietal placentæ are terminal and situated opposite one to the other. They are orientated laterally, not antero-posteriorly as described by Baillon, but they may occupy either position in the species with singly situated flowers, according as the single flower represents a median or a lateral member of the axillary groups of three present in *G. elliptica*. The styles should rest normally at right angles to the placentæ, but they are slightly twisted from this position in *G. elliptica*. They rest in the plane of the placentæ in *G. Veitchii* and *G. longifolia*.

A single descending ovule with "dorsal" raphe develops from each placenta. It becomes ultimately tangentially orientated. The nucellus is invested by a single integument.

The writer has been unable to follow the development of the nucellus, owing to the lack of suitable flowers. The first material examined consisted of fruits of the hybrid, *G. Thuretii*. Later, fertile fruits of *G. elliptica* were obtained. Finally, some flowers of this species were examined and the ovules removed and microtomed. These were in an advanced stage of development. The embryo-sacs were considerably elongated and sterile, having escaped fertilization. The basal part of the nucellus consisted of about five rows of cells; so that, in all probability, the young nucellus is comparable in bulk to that of *Cornus*.

Text-fig. 8.



Diagrams showing the course of the vascular tissue in the female flower of *Garrya elliptica*.
A, young fruit; B–F, flower. (For abbreviations see p. 308.)

Vascular Structure.

The vascular tissue of the pedicel consists of two opposite simple bundles (*d*) and two groups of small strands, which alternate with the former. The small bundles of each

group unite to form one (*m*), so that four (*d* 1, *d* 2, *m* 1, *m* 2) traverse the ovary-wall (Text-fig. 8, B). Each of the bundles *m* forms an ovular branch *o* (C), and then extending upward divides to form two (E, *m'*, *m''*), which become the opposite marginal bundles of the free styles (F); *d* 1 and *d* 2 become the median bundles of the corresponding styles (F).

The ovary corresponds closely to that of *Hamamelis* and other Hamamelidaceæ, consisting of two carpels with their respective traces, the adjacent marginal bundles being congenitally united.

Nature and Origin of the Flower.

Notwithstanding his interpretation of the morphology of *Garrya*, Lindley * found some difficulty in assigning it a systematic position. He first selected the "Urtical Alliance," but later decided in favour of the Helwingiaceæ, then recently established by Decaisne, and accordingly associated the monotypic family Garryaceæ with the Helwingiaceæ to form the alliance or cohort Garryales. Both families agree, writes Lindley, in possessing an epigynous calyx and a minute embryo embedded in copious endosperm.

Garrya, bearing the hall-mark of epigyny, is henceforth compared with epigynous forms, even by Baillon, who sceptically regarded Lindley's calyx. Baillon † included *Garrya* in his Cornaceæ. He supposed that the ovary, from an evolutionary point of view, is intermediate in structure between those of *Aucuba* and *Cornus*. This *Aucuba-Garrya-Cornus* series of his is analogous to that which he believed could be traced between the Combretaceæ and bilocular forms of *Marlea*.

It is now evident that the true nature of the flower has long been masked, owing to the vagaries of bracts. Bracts are inserted on the ovary-wall in several species, and in the common species, *G. elliptica*, reach an epigynous position. In *G. Fadyenii*, where the folioles do not exist, the perianth was supposed to have disappeared; thus Endlicher ‡ states, "perigonii in floribus pistilligeris vestigium nullum." Bracts, again, caused Bentham to err when he described opposite stamens in *G. laurifolia*: the stamens are alternate with the perianth segments. Finally, the close proximity of a pair of bracts to the perianth segments in the male flower led Harms astray, who believed that they represented a calyx.

The loss of the epigynous *calyx* or *perianth*, which had been considered homologous with the perianth of Cornaceæ, involves a total reconsideration of the whole problem.

Wangerin, influenced by the amentaceous inflorescence, diœcism, apetalous and hypogynous flowers, compares *Garrya* with *Salix*, *Betula*, *Juglans*, and *Myrica*, and removes it from the Cornaceæ to the restored Garryaceæ. This family, in Engler's revised Syllabus, is re-established in the Garryales, now situated between the Salicales and Myricales. Both Wangerin and Engler seem to have regarded certain characters as of little consequence—for instance, the basal "orthotropous" ovules of *Juglans* and

* J. Lindley, Veg. King. 2nd ed. 295.

† H. Baillon, Histoire des Plantes, vii. 82.

‡ S. Endlicher, Gen. Pl. Suppl. ii. 30.

Myrica and the exalbuminous seeds of *Salix*, *Juglans*, *Betula*, and *Myrica*. The ovules of *Garrya* are anatropous, and the seeds contain copious endosperm.

Again, since the embryology of *Garrya* is not yet understood, it would be wise to reserve a final judgment until a more thorough comparison with the Amentiferæ could be made, the embryology in the latter group being already known from the work of Benson and others.

Now genera with amentaceous inflorescences and diœcious, apetalous, hypogynous flowers occur also among *albuminous* families with *anatropous* ovules, and their ovaries are comparable in many cases to those of *Garrya*. Thus the resemblance to the Hamamelidaceæ is comparatively close. The structure of the ovule forms the only considerable difference. *Garrya*, in many features, is not unlike *Scepa*, now incorporated with *Aporosa*, a genus of the Phyllantheæ; but the Phyllantheæ are defined as possessing ovules with a ventral raphe, which is not the case in *Garrya*. Lastly, *Garrya* may be favourably compared with *Forstiera*, a genus of Oleaceæ.

(*e*) Helwingia.

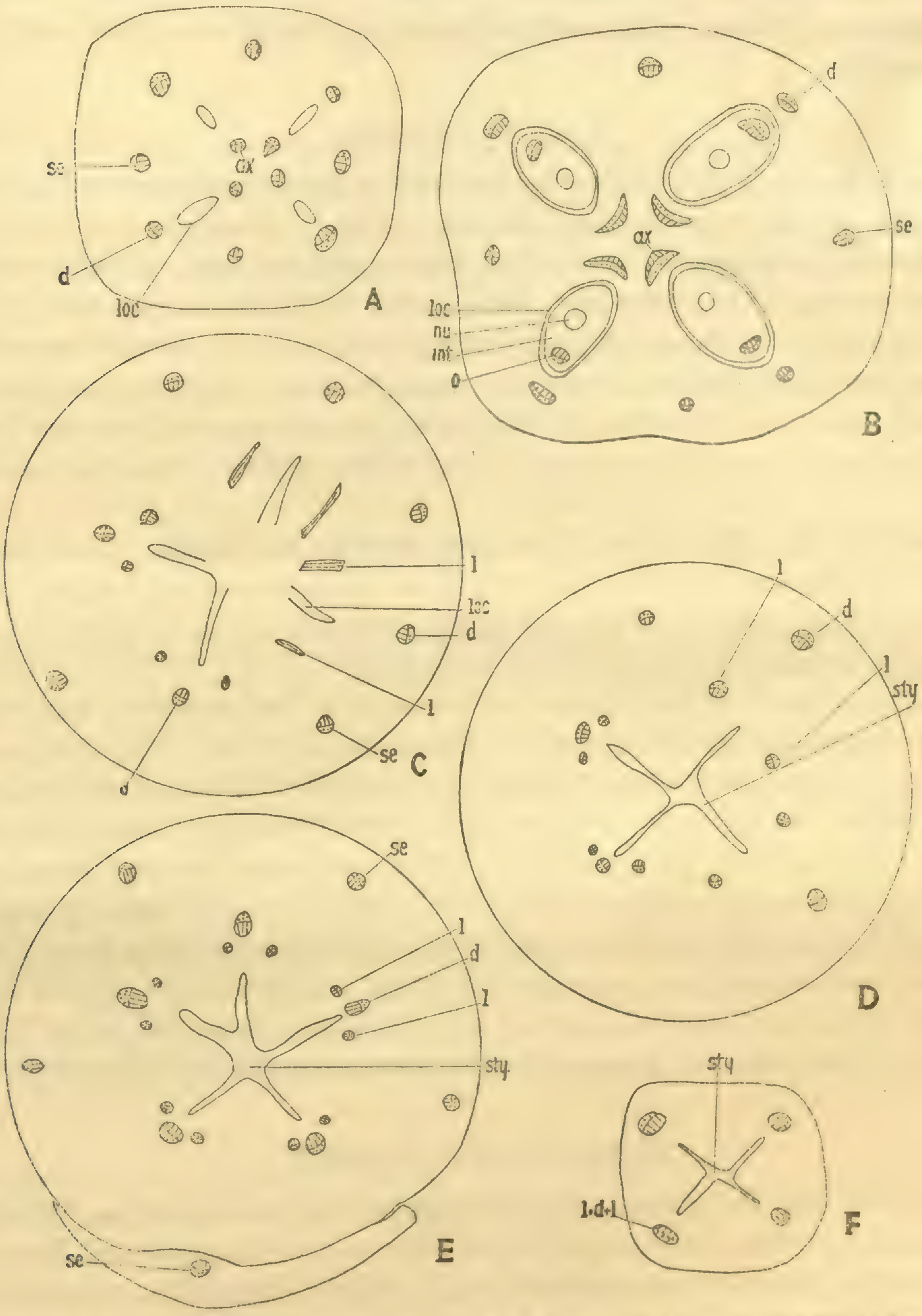
Morphology of the Flower and Ovule.

The flowers are unisexual and seated upon the midrib of a foliose bract. The male inflorescence consists of a group of separate pedicellate flowers, found to be either trimerous or tetramerous, both kinds being present in the same inflorescence. Each flower possesses a polyphyllous perianth and a single whorl of stamens, which alternate with the perianth leaves. The female inflorescence comprises a single, minutely pedicellate, epigynous flower, which bears at its base a small foliole. The flower consists of an inferior polycarpellary ovary terminated by free styles and surmounted by a single whorl of perianth leaves, resembling those of the male flowers, which alternate with the stigmas. Stamens, or the rudiments thereof, are entirely absent. Both whorls are usually tetra- or pentamerous, but in one exceptional case a pentamerous ovary was surmounted by a tetramerous perianth. The ovary is multilocular, each loculus containing a single, terminal, axially suspended, descending, anatropous ovule with abaxial raphe. The ovule is radially orientated, and since the nucellus of the mature ovule rests between the axial portion of the ovary and the abaxial raphe, the orientation is the inverse of that characteristic of the Araliaceæ, where the ovules are also radially orientated.

Owing to its radial orientation, vertical sections of the ovule are easily obtained. Such a section of the youngest ovule found is shown in Pl. 29. fig. 73. The integument shows no sign of dual origin. The nucellus approximates closely to the condition in *Lilium*, and consists of three short axial rows made up each of two or three cells. Pl. 29. fig. 73 shows a single enlarged subepidermal archesporial cell, of which the subsequent development has not been traced. The nucellus soon assumes the vertical position, owing to the activity of meristem at its base, and by the time the embryo-sac is formed the ovule has elongated considerably (Text-fig. 13, B).

This elongation is due to the activity of the lower cells of the nucellus, which, owing to the continuous formation of transverse partitions, give rise to vertical tiers of cells, so

Text-fig. 9.



Diagrams of transverse sections showing the course of the vascular tissue in the female flower of *Helwingia ruscifolia*. (For abbreviations see p. 308.)

that the nucellus expands longitudinally and provides for subsequent extension. Meanwhile, the lower rim of the integument increases by cell-division to form oblique rows (*int*), whilst the upper rim obtains only a small extension; hence the integument,

as a separate organ, forms only a small portion of the ovule, as in *Davidia*. Its boundary, *l*, is indicated in Text-fig. 13, B. The embryo-sac, as shown in Pl. 29. fig. 74, is immediately subjacent to the epidermis of the nucellus. Only one epidermal cell is shown in the figure, and no trace of a cap formed from sterile megaspores nor traces of parietal tissue are evident. The embryo-sac itself exhibits no noteworthy departure from the normal.

Vascular Structure.

The vascular tissue of the pedicel in the female flower separates into a peripheral and an axial (*ax*) series of bundles (Text-fig. 9, A). There are ten outer and five inner bundles in pentamerous flowers, but the number in each series varies with the carpels; in the case of the exceptional flower noted above (*Helwingia*, text, p. 278), the bundle corresponding to the missing sepal was absent. The bundles of the outer series opposite the loculi (B, *d*) take an upward course, without branching, into the style (F) and stylar lobes—one into each, corresponding to dorsal carpellary bundles; those alternating with the loculi (B, *se*) extend upward also without branching and enter the sepals.

The bundles of the axial series (B, *ax*) are opposite the loculi. Each one extends axially as far as the corresponding placenta, forms three branches of which the median becomes the ovular bundle, whilst the lateral branches (C, E, *l*) pass outwards, and ultimately join the corresponding dorsal bundle (F).

Two interpretations of the vascular structure may be presented, and until more extended investigations have been made claim equal attention. The first is suggested by a comparison with *Aralia* and *Nyssa*. As in *Aralia*, the traces are free, and when the number of carpels and perianth segments deviates from the normal the traces vary correspondingly. A transition from hermaphrodite to female flowers occurs in *Nyssa*, when both the stamens and stemonal traces disappear; so *Helwingia*, by analogy with *Nyssa*, may have lost both stamens and petals, together with their traces, when epigynous. The second and perhaps a more tempting solution is to suppose, by analogy with *Garrya*, that the flower was already apetalous and unisexual in its hypogynous state, in which case petal and stemonal traces have never existed in the ovary-wall.

Morphology of the Perianth.

Lindley * compares the perianth with the supposed calyx of *Garrya*. Bentham and Hooker †, on the contrary, hold that it is homologous with the corolla of *Meryta*, a genus of the Araliaceæ. Both genera are placed side by side in the Araliaceæ for the following reasons:—(1) The perianth leaves alternate with the stamens in both genera, and the æstivation is valvate; (2) in *Meryta* both calyx and corolla are present in the male flower, although the calyx is absent in the female flower. Bentham and Hooker deduce that the calyx, already obsolete in the female flower of *Meryta*, has entirely disappeared

* J. Lindley, Veg. King. 2nd ed. 295 (1847).

† G. Bentham et J. D. Hooker, Gen. Pl. i. (1867) 940.

in *Helwingia*. Now Bentham and Hooker state that the Cornaceæ and Araliaceæ are to be distinguished by the type of ovule prevailing in the family; so they were evidently unaware that the ovule, in *Helwingia*, does not conform to the Aralian type, with ventral raphe, and hence could not belong to the latter family. If, then, the genera are not closely related, the arguments bearing on the homology of the perianth diminish in value.

Another solution of the puzzle presents itself, however. It will be observed that the perianth leaves alternate with stamens in the male flower, corresponding in position to petals; but in the female flower they alternate with the stigmas, and might represent sepals. Now if the perianths of the male and female flowers are homologous, it is conceivable that some anomaly exists with regard to the stamens. If it were supposed that the flower was primitively ob- or diplostemonous, but has lost the inner or outer whorl of stamens, as the case may be, then the perianth segments could be interpreted as sepals and the orientation of the whorls in both the male and female flowers could be explained. Among Cornaceæ a double whorl of stamens has been recorded in *Nyssa sessiliflora*.

Comparison between Helwingia *and* Cornus.

Morren and Decaisne* established *Helwingia* in a new family, the Helwingiaceæ. This arrangement was subsequently criticised by Baillon†, who states that Decaisne was misled by artificial characters. Baillon points out that the female flower is constructed very like the flower of *Cornus*, and the ovules of both genera are of the same type. He considered that Bentham and Hooker, in placing *Helwingia* among the Araliaceæ, were led astray owing to the numerous agreements in character and organization between *Helwingia* and *Meryta*.

Now the ovules of *Cornus* (with dorsal raphe) are orientated tangentially—an orientation that appears to be constant for the Caprifoliaceæ; whereas those of *Helwingia* (with dorsal raphe) are radially orientated, and the position taken up in the loculus seems to be the outcome or result of a genetic difference in the ovule, as explained by the writer in a previous paper. Hence the ovules of the two genera are not necessarily homologous, as considered by Baillon.

Again, the vascular systems do not correspond. That of *Helwingia*, owing to the existence of separate perianth and dorsal carpellary bundles, agrees more nearly with the Aralian type. The vascular supply to the ovule is different in the two cases. In *Helwingia* each axial bundle divides to form three, of which the median enters the ovule; in *Cornus*, lateral branches from a pair of opposite peripheral bundles unite to form the ovular trace. These details show that the resemblances between the two genera are not so real as Baillon supposed, and that he himself was influenced by structural parallelisms.

* Morren et Decaisne in Bull. Acad. Brux. v. (1836) 169.

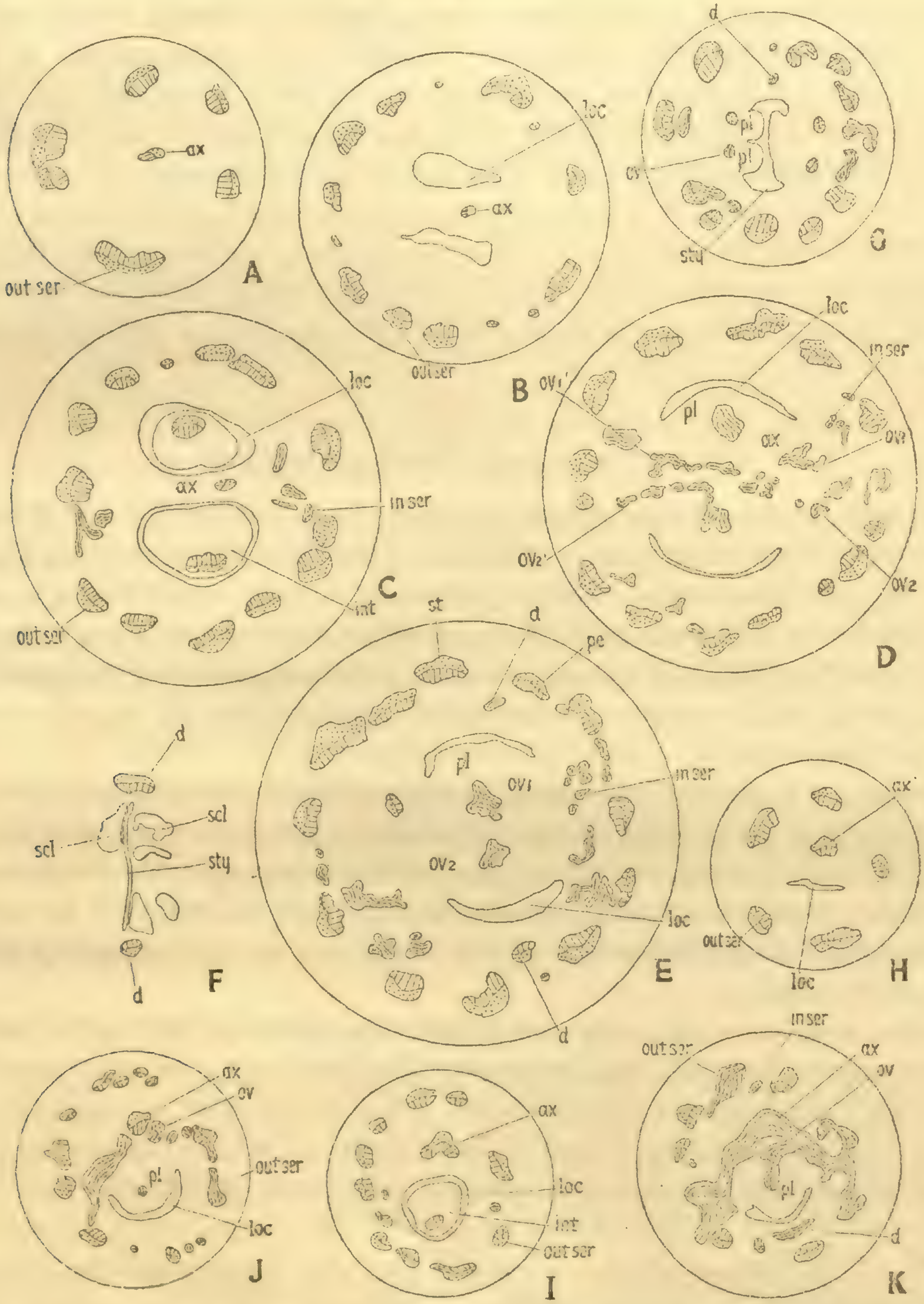
† H. Baillon in Bull. Soc. Linn. Paris, i. (1877) 137.

(*f*) Corokia.

Morphology of the Flower and Ovule.

The flowers of *Corokia Cotoneaster* are hermaphrodite, with epigynous pentamerous whorls of sepals, petals, and stamens. The ovary is usually unilocular, sometimes

Text-fig. 10.



Diagrams showing the course of the vascular tissue in the flower of *Corokia Cotoneaster*.
(For abbreviations see p. 308.)

bilocular. The style consists of two congenitally united units in bilocular forms. The

stylar canal is cross-shaped (in bilocular forms), and upon tracing it downwards the longer arm passes into communication with the loculi and the shorter arm is distinctly sutural. The canal is sometimes three-lobed in unilocular ovaries.

The terminal ovules in bilocular ovaries are axially suspended, one in each loculus; but traces of parietal placentæ, absent in *Cornus*, exist immediately above the point of insertion of the ovules (Text-fig. 10, G, *pl*). The ovules are radially orientated, as in *Helwingia*. The orientation is not disturbed in relation to the absence of the septum.

Vascular Structure.

Several hand-cut series and one by the microtome were prepared through unilocular ovaries, whilst two series by hand and one by the microtome were taken through bilocular ovaries. The last-mentioned microtomed series will now be described. Six peripheral bundles (*out ser*) and one centrally-situated or axial bundle were present below the loculus (Text-fig. 10, A). The peripheral bundles, branching and anastomosing, increase upward to form an outer series of twelve bundles which are the traces of six petals and six stamens, and some small inner branches (B–E). The majority of the inner branches arise from the bundles near the septum on either side (D). They extend into the septum, and strands from opposite sides (*ov* 1, *ov* 1′, and *ov* 2, *ov* 2′) augmented by the axial bundle (*ax*) unite to form the ovular trace. Two bundles extend upward from this level, but soon die out (E). In another flower four bundles were present at a corresponding level, one in each placenta (G, *ov*). Two of the above-mentioned inner branches (E, *d*) extend upward and occupy a dorsal position in the style (F).

In unilocular ovaries, the "axial" bundle is situated near the side of the loculus (H, I). It extends upwards and is joined by inner branches corresponding to those marked *ov* in D, so that an irregular arc or collar of vascular tissue is formed (J, K) from which the ovular trace arises.

The change to the unilocular condition is accompanied by the displacement of the axial bundle, and by the diversion of the vascular tissue pertaining to the absent ovule to the present ovule.

Comparison with Cornus.

Corokia was described by A. Cunningham * in 1839. Endlicher † at first placed it near the Rhamnaceæ, but later ‡ transferred it to the Cornaceæ, and it remains in this family in the systems of Bentham and Hooker, Baillon, Harms, and Wangerin. *Corokia*, however, differs from *Cornus* in the following details:—(1) the presence of parietal placentæ immediately above the situation of the ovule; (2) the existence of an axial bundle; (3) the method of vascular supply to the ovule, and (4) orientation of the ovule. Hence the structural agreement is not quite so close as hitherto supposed.

* A. Cunningham in Ann. Nat. Hist. iii. (1839) 249.

† S. Endlicher, Gen. Pl. 1103 (1840).

‡ S. Endlicher, Gen. Pl. Suppl. iv. pt. 3, 18 (1850).

(*g*) Melanophylla.

This genus was first described by Baker * in 1886. Two species—*M. alnifolia* and *M. aucubifolia*—were recorded. According to Baker's description, the flowers are hermaphrodite with alternate pentamerous whorls of sepals, petals, and stamens. The ovary is bi- rarely trilocular and the styles bi- or trifid. The loculi are uniovulate, Baker † described a new species, *M. crenata*, in 1896 with illustrations. Figures from specimens of this species in the Herbarium Boissier are given by Wangerin ‡ in 'Das Pflanzenreich.' Only one loculus is shown in both Baker's and Wangerin's illustrations.

Baker, in 1886, states that two species of *Melanophylla* are comprised in Humblot's collection from the north-east portion of the island of Madagascar. Now in 'Plantes de Madagascar' §, a new species, *M. Humbloti*, is figured which is evidently one of those mentioned by Baker. This species is not recorded in 'Das Pflanzenreich' and no written description seems to have been published, but it is mentioned in Palacký's ‖ 'Plantarum Madagascariensium.' According to the figures of *M. Humbloti* the stigmas, which are tongue-shaped, are not recurved as in Baker's species—the calyx is depicted with a waved rim and not with definite segments as in *M. crenata*, and there are slight differences in the ovary and the stamens. Only one loculus and one ovule are figured.

Wangerin associates *Melanophylla* with *Griselinia* to form a new tribe of Cornoideæ, the Griselineæ.

(*h*) Griselinia.

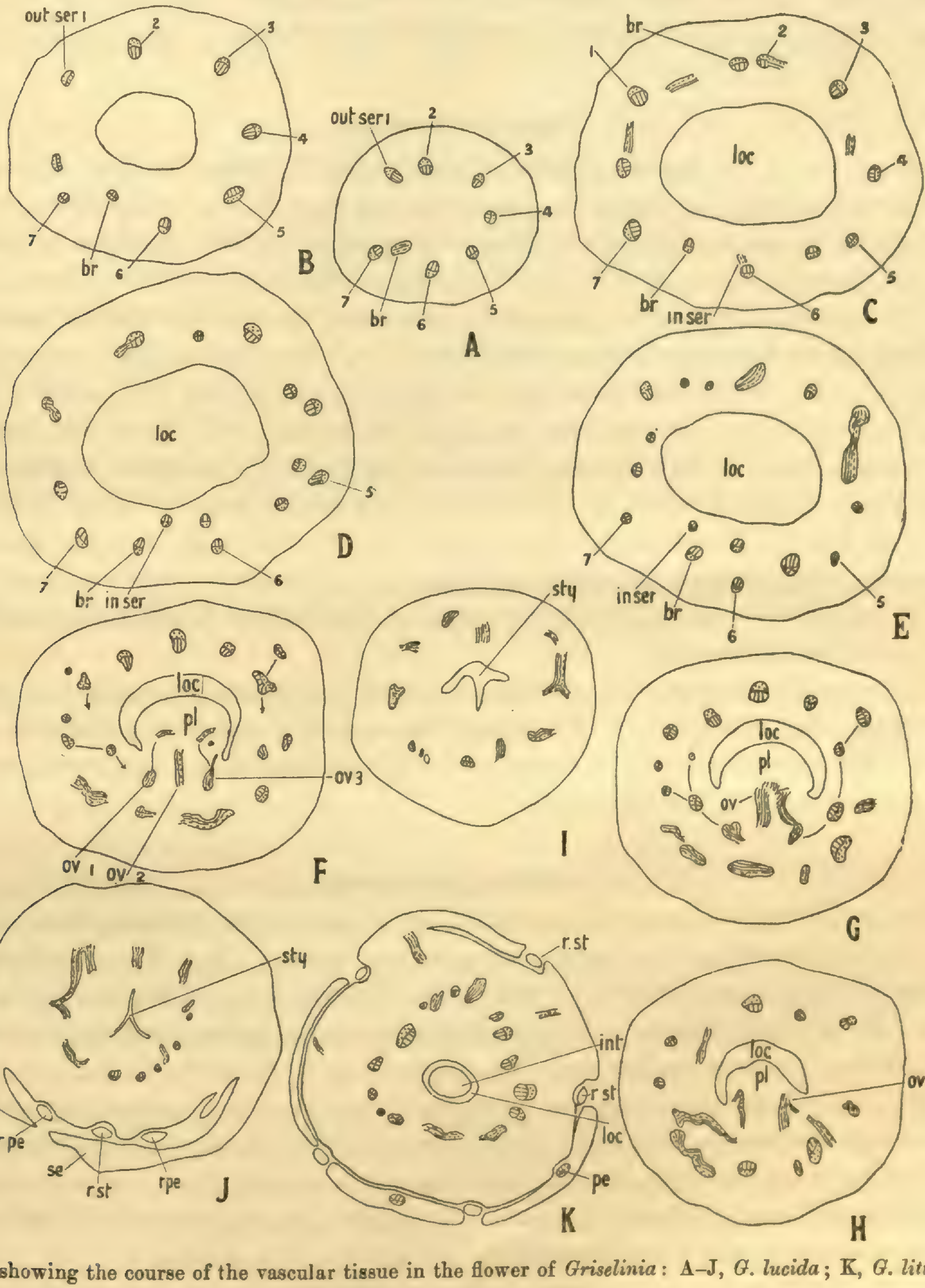
Morphology of the Flower and Ovule.

The plants and flowers of *Griselinia* are unisexual. The male flowers of *G. littoralis* and *G. lucida* consist of sepals, petals, and stamens in alternating pentamerous whorls, which surround a flat circular disc with five or six grooves radiating outward from the centre. Ovarian rudiments are absent. The female flowers are epigynous, and surmounted by sepals and petals in *G. littoralis* and by sepals only in *G. lucida*. The petals are imbricate. Stamens are absent in all the species. Bentham & Hooker ¶ and Wangerin ** state that there are no rudiments of stamens, and none have hitherto been recorded. The writer finds not only rudiments of stamens in *G. littoralis* and *G. lucida*, but rudiments of the absent petals in *G. lucida*. These are very minute, but they can be observed with the aid of a good pocket-lens. Text-fig. 11, K, represents a transverse section of *G. littoralis*; here the positions of the petals are denoted by

* J. G. Baker in Journ. Linn. Soc., Bot. xxi. (1886) 352.
† J. G. Baker in Hook. Ic. Pl. xxv. (1896) pl. 2499.
‡ W. Wangerin in Das Pflanzenr. Heft 41, 100.
§ H. Baillon in 'Plantes de Madagascar,' Atlas, iii. pl. 400 (1896).
‖ Palacký in Plant. Madagasc. fasc. iv. (1906) 50.
¶ G. Bentham et J. D. Hooker, Gen. Pl. i. 951.
** W. Wangerin in *l. c.* 95.

pe, and the rudiments, five in number, occur just within the sepals, occupying the position of stamens (*r st*). The rudiments of stamens and petals in *G. lucida* are

Text-fig. 11.



Diagrams showing the course of the vascular tissue in the flower of *Griselinia*: A–J, *G. lucida*; K, *G. littoralis*.
(For abbreviations see p. 308.)

shown in J. The ovary is terminated by three styles. It is unilocular or bilocular according to Bentham and Hooker *. Wangerin † describes only one loculus. The

* G. Bentham et J. D. Hooker, Gen. Pl. i. 951.

† W. Wangerin in Das Pflanzenr. Heft 41, 95.

writer finds no bilocular ovaries in his material of *G. lucida*. The ovular mamelon grows downwards and develops into an ovule of the abaxial type. The orientation in bilocular ovaries has, of course, not been observed. The nucellus, which is comparatively long, is of very small bulk—a median section shows three rows of cells within the nucellar epidermis ; it is invested by a single integument (Pl. 29. figs. 75, 76).

Vascular Structure.

Serial sections of the flowers of both *G. lucida* and *G. littoralis* were prepared. In *G. lucida* six or seven bundles were present at the base of the ovary (Text-fig. 11, A). These branch to form a single series, consisting of a variable number of bundles—twelve or more—in the ovary-wall (B–F). Some of the smaller bundles extend inward, and in the neighbourhood of the placenta anastomose, presenting in thick sections the appearance of an incomplete vascular collar (F–I) ; from this "collar" as many as five separate bundles, of which three (*ov* 1, *ov* 2, *ov* 3) are shown (F), extend into the "placenta" and unite there to form the single ovular bundle. Since the petals and stamens are absent in this species, there are no outgoing branches to these organs, and all the principal bundles, together with a few which proceed from the "collar," extend into the basal portion of the style (I, J), diminishing in number until only a few remain. The vascular structure is similar in *G. littoralis* (petals present), except that the bundles are more numerous—nine at the base of the loculus and sixteen higher up in one specimen.

The vascular structure in the neighbourhood of the placenta recalls the somewhat similar collar-like arrangement of vascular tissue in the reduced unilocular ovary of *Corokia*. In *Griselinia*, however, branches from every part of the ovary-wall contribute to the bundles entering the "placenta."

Nature of the Ovary.

Baillon considered the ovary of *Griselinia* to be incompletely tricarpellary, the body of the ovary consisting of the lower portion of one carpel. But the peculiar vascular structure justifies a modification of this view. When we consider the cases already discussed, it is found that where the terminal ovule is by origin axially situated the vascular tissue presents an anomaly, but where it is parietally situated by origin the conditions are not the same and the vascular tissue need not necessarily be diverted from the normal course. Thus, in *Viburnum*, the ovary was primitively septate, but, owing to the loss of the septa, the vascular tissue that had originally an axial extension became diverted to a peripheral position. Again, in *Corokia*, where in bilocular forms the ovules are suspended from the septum, the absence of a loculus disturbs the normal disposition of the vascular tissue in relation to the ovule. But in *Aucuba*, also originally septate, where the ovule is suspended from a parietal placenta and comparable to the parietally situated ovules in the Combretaceæ, no vascular anomaly exists in relation to the position occupied by the ovule. Now, in *Griselinia*, the placenta is abnormally large, and the numerous branches contributing to the ovular trace arise from bundles

extending in all parts of the ovary-wall, and appear to have been diverted from the original disposition. Hence not only can we deduce that the ovary was primitively septate, but also that the ovule was axially placed.

Now, abortion, in *Viburnum*, originally tricarpellary, has conduced to the special development of the body of one carpel, a fact that is evident from the asymmetrical disposition of the vascular tissue in the flower and from the arrested loculi. But, in *Griselinia*, as also in *Corokia* and *Aucuba*, the original course taken by the floral vascular tissue does not appear to have been affected by abortion. Hence the conclusion is reached that the septa disappeared without a special enlargement of the lower portion of any one carpel.

The writer's interpretation of the floral structure may be summarized briefly as follows:—The flower was primitively hermaphrodite, and became unisexual after the attainment of epigyny; it exhibits an apetalous tendency, definitely expressed in *G. lucida*, the ovary was originally tricarpellary and trilocular, and the loculi, by analogy with the Caprifoliaceæ, were at first pluriovulate. Subsequent abortion resulted in the disappearance of the septa, but did not induce the special enlargement of the lower portion of any one carpel, as in *Viburnum*; concurrently, the ovules were numerically reduced to one, the equivalent of an axially suspended ovule in the primitive ovary. If Baker's record of bi- and trilocular ovaries in *Melanophylla* be correct, we may conceive that *Griselinia* has proceeded a stage further than *Melanophylla* in the direction of abortion.

(*i*) Nyssa.

Morphology of the Flower and Ovule.

The flowers of *Nyssa* are hermaphrodite or unisexual. The male flowers consist of sepals, petals, and stamens, which vary from five to an indefinite number. According to Bentham and Hooker *, ovarian rudiments are absent or a subulate process exists in the centre of the disc. The female flowers consist of an inferior ovary surmounted by a calyx—petals are absent or minute and there are no rudiments of stamens—and terminated by one or two styles. The flowers of *N. sylvatica*, growing at Kew, which the writer examined, proved to be either hermaphrodite or female. The hermaphrodite flowers possessed one, two, or three stamens, so that a complete series existed between the two kinds.

Bentham and Hooker † state that the ovary is unilocular, but Baillon ‡ records that it may be sometimes bilocular. The writer has observed only unilocular ovaries in *N. sylvatica*. The ovule is terminal in mature ovaries, but this is not strictly so in very young flowers; in one particular case measurements were made with the aid of a series of sections, each ·015 mm. thick; the height of the loculus was 0·24 mm.; the total length of the ovule 0·165 mm. The ovule was attached to the ovary-wall at a point

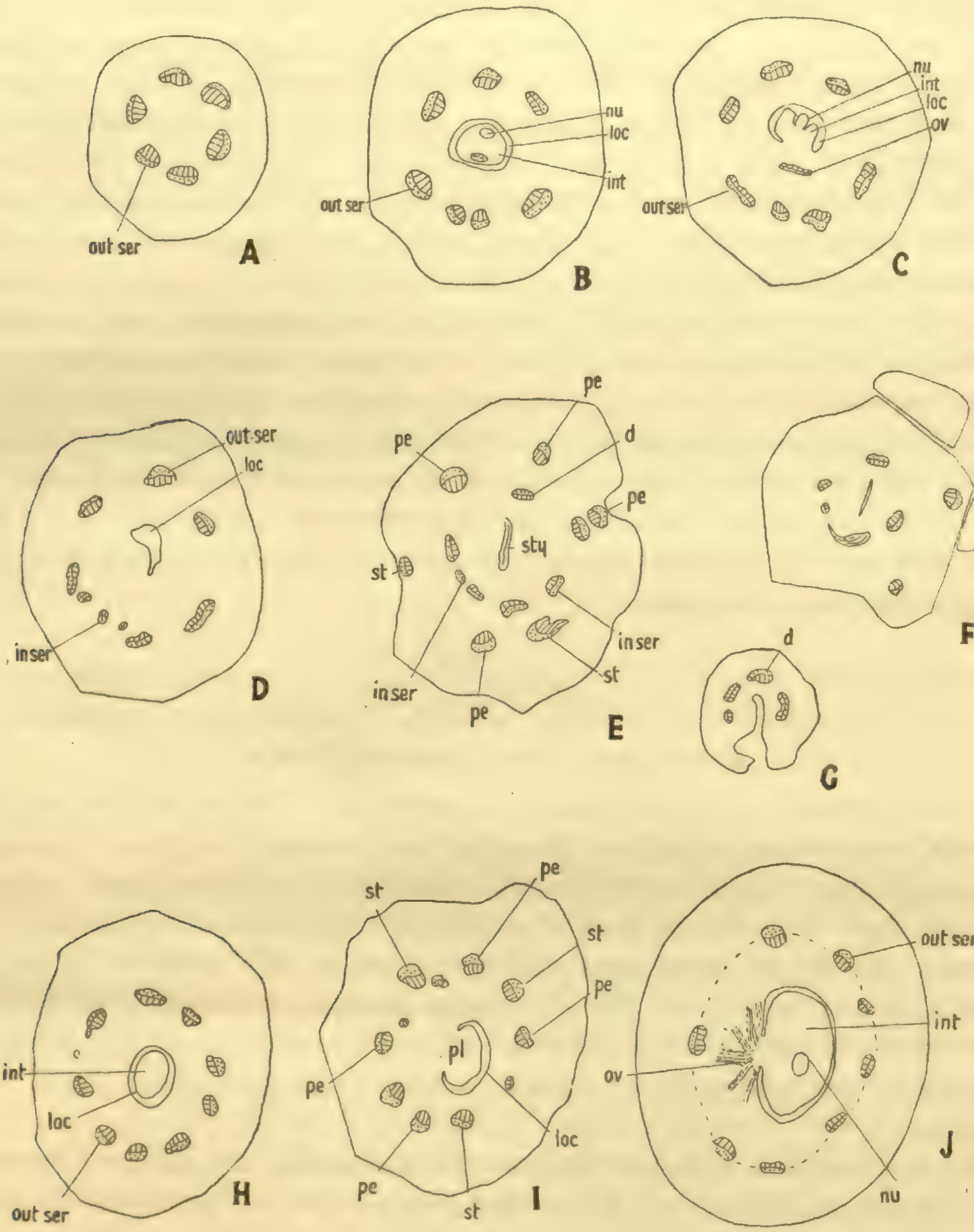
* G. Bentham et J. D. Hooker, Gen. Pl. i. (1867) 952.

† G. Bentham et J. D. Hooker, *l. c.*

‡ H. Baillon, 'Histoire des Plantes,' vi. 267.

about 0·08 mm. from its own summit and the top of the loculus. It is of the adaxial type and comparable to that of *Davidia*. Wangerin states that two integuments are present, but the writer finds only one (Pl. 29. fig. 77). The nucellus is of small bulk

Text-fig. 12.



Diagrams showing the course of the vascular tissue in the flower of *Nyssa sylvatica*.
A–G, one flower; H, I, another flower; J, fruit. (For abbreviations see p. 308.)

and comparable to that of *Davidia*, but its further development has not been followed, owing to the lack of suitable material.

* W. Wangerin in Das Pflanzenreich, Heft 41, p. 9.

Vascular Structure.

Serial sections through very young flowers and hand-sections of sterile "fruits" were prepared from only one species—*N. sylvatica.*

In one flower six bundles were present in the lower portion of the ovary (Text-fig. 12, A), these extended upward toward four petals, *pe*, and two stamens, *st* (B–E); in another, nine bundles occurred (H), but only seven of these supplied stamens (three) and petals (I).

An inner series of fine branches originates from the cylinder of bundles near the point of attachment of the ovules (D, E) and extends into the style (F). The branch *d* occupies a dorsal position in the style, but the flowers were too young to show the vascular connections of the ovule, hence the nature of the remaining branches could not be determined. From sections of fruits it appears that two or three strands unite to form the ovular bundle (J).

Owing to the variability in the flower in the genus, a comparison needs to be made with the remaining species before the significance of the vascular peculiarities can be adequately discussed.

Comparisons.

Endlicher* placed *Nyssa* in a new family, the Nyssaceæ, near the Santalaceæ. Baillon† transferred it to the Combretaceæ for reasons similar to those which influenced him in attaching *Alangium* to this family. But the occasional presence of two styles, one of which is rudimentary in *N. sylvatica*, and the recorded case of a second incomplete loculus indicate that the ovary is unilocular by abortion. Bentham & Hooker‡ and Harms§ include *Nyssa* among the Cornaceæ, but it differs from *Cornus* in possessing the Aralian type of ovule, in its variable flowers, imbricate corolla, free styles, and reduced ovary. Wangerin‖ separates it from the Cornaceæ on the ground that the ovule is bitegumentary, but since the ovule possesses only one integument this criterion fails.

Nyssa approaches *Aralia* in the form of ovule (adaxial). But the ovules of *Aralia* are parietally borne, whereas the ovular bundles of *Nyssa*, by analogy with *Griselinia*, might indicate that the ovule was originally axially suspended. A closer structural agreement exists between *Nyssa* and *Davidia*, both genera possessing polygamous flowers, free styles, and numerous stamens.

Summary.

1. The following details of floral morphology are recorded:—
   - *a.* The occasional occurrence of hermaphrodite flowers in *Aucuba himalaica.*
   - *b.* Biovulate ovaries in *A. japonica* and *himalaica.*
   - *c.* Anomalous flowers in the hybrid *Garrya Thuretii*—these consist of three congenitally united flower-heads borne upon one "pedicel," thus combining

* S. Endlicher, Gen. Pl. 328.
‡ Bentham et Hooker, Gen. Pl. i. 952.
‖ W. Wangerin in Das Planzenr. Heft 41, 9.
† H. Baillon, Bull. Soc. Linn. Paris, i. (1877) 271.
§ Harms in Engl. u. Prantl, Nat. Pfl. Teil iii. Abt. 8, 257.

the characters of both parents, viz., *G. elliptica* in which the flowers occur in axillary trimerous groups, and *G. Fadyenii* in which they are situated singly in the axil of each bract.

d. Rudiments of a single whorl of stamens in the female flowers of *Griselinia littoralis* and *lucida* and of the absent petals in *G. lucida*.

e. Rudimentary terminal parietal placentæ in *Corokia Cotoneaster*.

2. The terminal ovules are suspended axially in *Davidia*, *Cornus*, *Helwingia*, and in bilocular forms of *Marlea* and *Corokia*; probably axially by origin in *Nyssa* and *Griselinia*, and parietally borne in *Aucuba* and *Garrya*.

3. The ovule exhibits considerable variety in organization :—

a. It is in *Nyssa* and *Davidia* of the dorsal type (raphe ventral or adaxial) with radial orientation ; of the ventral type in *Helwingia* and *Corokia* (raphe dorsal or abaxial) with radial orientation, but the inverse of the former ; and of the ventral type with tangential orientation in bilocular forms of *Cornus* and *Marlea*.

b. The nucellus in the genera investigated (including *Davidia* and *Nyssa* deseribed as bitegumentary by Harms and Wangerin) becomes invested with a single integument.

c. The integument is completely free from the nucellus in *Aucuba* and *Griselinia*, but in the specialized ovules of *Davidia* and *Helwingia* is only found as a separate organ towards the summit of the nucellus.

d. The nucellus consists of about seven axial rows of cells in *Aucuba*; four or five in *Cornus*, *Davidia*, *Griselinia*, and *Garrya* ; and three in *Helwingia*, where it approximates to the condition obtaining in *Lilium* and *Inula*.

e. The nucellus of *Aucuba*, in the formation of a definite layer of parietal tissue, a small epidermal cap, and in subsequent bulk-extension owing to cell-division, approaches the type described by Péchoutre for the Rosaceæ.

f. The germination of more than one megaspore, already recorded by the writer for *Davidia*, occurs also, but not to the same extent, in *Aucuba*.

4. The floral vascular systems of the Cornaceæ do not conform to one type as in the Caprifoliaceæ. It is in *Cornus* of the Caprifoliacean type. The systems of *Griselinia*, *Nyssa*, and *Helwingia* exhibit Araliacean tendencies; those of *Davidia* and *Marlea* are transitional in character between that found in *Aralia* and the synthetic systems of *Cornus* and the Caprifoliaceæ. The stage of economical advance reached by *Viburnum* has not been attained.

a. Infra-locular extensions of vascular tissue occur in *Aucuba* and unilocular forms of *Marlea*.

b. The ovular trace is anomalous in *Griselinia*, *Nyssa*, and unilocular forms of *Corokia*.

c. Branches from the ovular trace traverse the peripheral region of the integument in *Davidia* and *Corokia*.

5. The flowers of certain genera admit of the following interpretation:—

a. Cornus: The ovary is bilocular by reduction from a quadricarpellary primitive type. It is analogous to that of *Sambucus*.

b. Alangium: The ovary is unilocular by reduction from the bilocular type found in *Marlea begonifolia*, and reduced from a form primitively polycarpellary.

c. Aucuba: The flowers have become unisexual since the attainment of epigyny. The ovary was primitively quadricarpellary and quadrilocular. The septa subsequently disappeared, but the lower portion of the carpels remained unmodified. The ovules, originally numerous, became numerically reduced until only a single parietally suspended one remained.

d. Garrya: The flower is hypogynous as already noted by Wangerin.

e. Griselinia: The flowers have become unisexual since the attainment of epigyny, and a tendency towards apetaly finds its expression in *G. lucida*. The ovary was primitively tricarpellary and trilocular, at all events in its upper portion, but the septa disappeared, leaving the lower portion of the carpels unmodified, but involving the displacement of an ovule that was primarily axially situated.

6. Progressive abortion in the ovary reaches its limit in this family—the ovaries of *Davidia* and *Helwingia* are multilocular, the change from the bi- to the unilocular condition can be traced in *Corokia*, and the ovaries of *Aucuba*, *Nyssa*, *Alangium*, and *Griselinia* are unilocular.

7. Progressive sterilization has proceeded still further than in the Hamamelidaceæ and Caprifoliaceæ, nearly all the genera have reached the level of the extreme cases in these families, and the ovary or loculus is absolutely uniovulate.

8. The general series that has been traced in the direction of the loss of carpellary autonomy culminates in *Aucuba*, where, owing to the absence of septa and to the parietal situation of the ovule, the gynæcium appears to consist of a single carpel.

9. Both the Cornaceæ of Harms and the Cornaceæ of Wangerin are heterotypic, but this fact is masked, owing to parallel development and convergent organization.

5. FINAL DISCUSSION.

The Interpretation of Resemblances and Differences.—Hitherto that which may be called the Principle of Resemblances has held amazing sway. Drawing first breath, as it were, in the days of Ray, virile before the birth of the 'Origin of Species,' it has evolved through the length of two centuries, and reached its zenith as presented by Adolf Engler in 'Die Natürlichen Pflanzenfamilien' just over twenty years ago. Almost on the eve of the publication of Engler's mighty work, a new era in botanical history had dawned. In 1889, De Vries's 'Intracelluläre Pangenesis' had been given to the world, an essay which Bateson * declares "remarkable as a clear foreshadowing of that conception of *unit-characters* which is destined to play so large a part in the development of genetics," to be swiftly followed by 'Die Mutationstheorie' †; whilst the year 1900 brought with it the triple rediscovery of Gregor Mendel.

* W. Bateson, Mendel's Principles of Heredity,' 5 (1913).

† H. De Vries, 'Die Mutationstheorie' (1901–3).

As the incidence of the 'Origin of Species' shed transcendent light upon the mystery of the Natural System in 1859, so the work of these great protagonists in experimental evolution, and the expositions emanating from the schools of experiment and thought founded by them, cannot fail in time to illuminate Systematic Botany and inaugurate a new phase in the evolution of the idea of the Natural System.

De Vries by a rigid analysis of *Œnothera* separated numerous diverse forms breeding true, some exhibiting comparatively great differences. The Mutation theory postulates the evolution of forms progressively divergent. Hence it is conceivable that forms—for instance, genera grouped in different families—are in some cases comparatively closely related. Again, the characters exhibited by De Vries's mutant Œnotheras are paralleled in other mutating races—for example, giantism in *Œnothera gigas* also occurs in *Lathyrus odoratus* (Bateson, 1909), *Pisum sativum* (Mendel), and in *Primula sinensis* (Keeble, 1912). Facts of this kind serve to redirect attention to the importance of the doctrines of parallel development and convergence in relation to floral evolution, especially since the surviving natural races trend in the direction of synthetic and economic advance. Convergence in reproductive characters may occur even more frequently than has yet been contemplated, so that like forms, such as genera in the same family, may be less closely related than others are that differ more pronouncedly. Hence the Principle of Resemblances must now be qualified by a greater regard for the significance of differences, even if it be not shaken to its foundation by the doctrine of convergence and the existence of insidious parallelisms.

Before proceeding to attempt to solve the phylogenies of the families considered here, it will be convenient to review the evolutionary processes that have been discussed in relation to the results obtained by the experimentalists. But the prospect is by no means encouraging, since De Vries* writes: "The great lines of evolution of whole families and even of genera and of many larger species obviously lie outside the limits of experimental observation. They are the outcome of the history of the ancestors of the present types, and a repetition of their history is far beyond human powers."

The carpels in *Davidia* vary from five to ten, with a mean number of six or seven; they vary in number in the forms of *Hedera Helix*; and, in *Sambucus*, species are characterized by five, and a range of from two to four with a mean of three respectively.

Mutation in the carpels has not yet been specially mentioned as occurring in the races produced by experiment.

Syncarpy supervenes upon apocarpy, and the advance towards syncarpy is accompanied or followed by that towards perigyny and epigyny, but here again there is as yet little direct experimental evidence.

The most fascinating phenomena are those attendant upon sterilization. A vast number of instances are known in which sterility is probably due to seasonal conditions, or to diversion or poorness of the nutrient supply, including the very numerous cases where only few of very many flowers develop in the inflorescence. *Davidia*, where all the ovules in the ovary may be fertile or sterile, may be included in this category. Thence we pass to numerous other cases in which it is doubtful whether sterility has

* H. De Vries, 'Species and Varieties' (1905) p. 223.

become definitely fixed or not; as in *Lonicera*, where the majority of the ovules habitually abort; in *Polyosma*, where, according to Blume, only one of the numerous ovules forms a seed; in *Liquidambar*, where the lowermost ovules are stated to be always sterile; in *Aralia* and *Corylopsis*, where one of a pair, and in *Quisqualis*, where one of three ovules is sterile. And, finally, cases occur, exemplified by *Symphoricarpus*, where the sterility of particular ovules is no longer a matter of circumstance, having become fixed and hereditary.

Sterilization proceeding to an extreme leads to unisexuality; thus in the Hamamelidaceæ series exist between forms in which the ovary may or may not be sterile, to others with definitely polygamous flowers and others where the unisexual condition is attained; in *Nyssa*, series can be traced between hermaphrodite and female flowers owing to the loss of stamens; in *Griselinia*, *Aucuba*, and *Garrya* rudiments of the absent sex are retained, but the last traces have disappeared in *Helwingia* and in the male flowers of *Davidia*.

A great deal of light has been thrown on the series just enumerated by the results obtained in the experimental fields of enquiry. De Vries*, by his analysis of ever-sporting varieties, was able to show how profoundly the environment affects development. Here the primordium of the flower in Polycephalic Poppies was influenced by changed conditions applied within the fifth or sixth week after the beginning of germination, and fewer anomalous stamens were produced than under normal conditions, whilst the occurrence of polycotyly and polycephaly in polycotylous and polycephalous half-races did not become definitely fixed during cultivation and selection. The phenomena concerned variability, not mutability. He† also found that the development of the anther and pollen in *Œ. scintillans* was dependent on external conditions to a high degree. De Vries's‡ *Œnothera* mutants show clearly grades of sterility. Some are rich in pollen, whilst *scintillans* is poor; others form many seeds, some few, as in *elliptica*, whilst in *brevistylis* many plants set no seed at all, but he believes the degree of fertility in many mutants will ultimately be found to follow Quetelet's law of fluctuating variability. Finally, with regard to sex sterility, unisexuality is exhibited by ever-sporting varieties, mutants, and Mendelian hybrids. R. P. Gregory§ records that no stamens occur in one of the double forms thrown off by *Primula sinensis*; and E. R. Saunders‖ has shown that the gynœcium in double Petunias is more or less deformed and when fertilized yields no seed, whilst double¶ stocks are always sterile and are always obtained from seed set from ever-sporting singles. De Vries** obtained a male sterile mutant, *Œnothera lata*. Lastly, Bateson††, Punnett, and Saunders, working with Sweet Pea, and Salaman‡‡, with Potato, have isolated male-sterile Mendelian forms.

* H. De Vries, 'Species and Varieties' (1905) 369, and 'Mutation Theory,' ii. (1910) 343, 450.

† H. De Vries, 'Mutation Theory,' i. (1910) 383.

‡ H. De Vries, *l. c.*, *scintillans*, 383; *elliptica*, 396; *brevistylis*, 316.

§ R. P. Gregory in Journ. Gen. i. (1911) 90.

‖ E. R. Saunders in Journ. Gen. i. (1911) 63.

¶ E. R. Saunders in Journ. Gen. i. (1911) 304.

** H. De Vries, *l. c.* 409.

†† Bateson, Punnett, & Saunders in Rept. Govt. Com. Roy. Soc. iv. 16.

‡‡ Redcliffe N. Salaman, in Journ. Linn. Soc., Bot. xxxix. (1910) 301.

The facts that the number of chromosomes may vary in mutants, as recorded by Gates * (1907) and later by Anna M. Lutz † (1907) for *Œnothera*, and that giantism is accompanied by increase in cell-size as first shown by Gates ‡ (*Œnothera*), and later by Keeble § (*Primula*), show the depth as well as breadth of the new aspect of things. It is hardly possible, therefore, to exclude the ovule from the possibilities of mutation. The change and grades of change from orthotropy to anatropy, the origin of the single and double integument, and even the change from many to few axial rows may yield in turn to patient and persistent experimental endeavour.

We are now able to conceive the origin of mutants in floral characters. Mutants might arise, for example, from apocarpous forms bearing some few and some many carpels. These could in time produce new species. If both the floral and vegetative organization alter considerably during the continuance of mutation, forms would arise exhibiting still greater divergence. But the advent of syncarpy and epigyny again and again in different families, and the frequent occurrence of sterilization in both Monocotyledons and Dicotyledons, culminating time after time in the evolution of uniovulate ovaries, whilst increasing enormously the tale of floral diversity, nevertheless contribute toward the evolution of synthetic and convergent structures.

Origins.—The interpretation of phylogenies must be influenced by views of origin, and the origin of new forms, as postulated by the Mutation Theory, is to render the recognition of affinities more problematic than ever. It is the custom to sort plants into divisions and groups according to this or that bias, and to construct a phylogenetic twig or branch of the great tree of descent; but the Mutation Theory brings home to us that that which is actually accomplished in Systematic Botany is the aggregation or linking of species, genera, and even families, as the case may be, that have attained a similar level in evolution, a similar resultant effect of racial experiences. These aggregations may or may not be related. The Compositæ, for example, form a homogeneous group consisting of genera in the same phase of synthetic and economic development; but is it certain that the members of the family are bound by the bonds of relationship, and are traceable to a single progenitor?

A general device in Comparative Morphology is to seek for clues to an interpretation of the origin of a structure from morphological series, and thence deduce a concept of affinity. But spacial series may not necessarily coincide with series in time, as exemplified by the sterilization series in the Caprifoliaceæ and De Vries's Œnotheras, where one form has not passed into another form, but each one has originated separately. Some points, however, carefully chosen, may establish unlooked-for differences. Thus the situation of the sole surviving seed is constantly parietal in the Hamamelidaceæ and axial in the Caprifoliaceæ. Hence in the Cornaceæ, where genera occur with either the parietally or axially borne seed, there is a strong bias towards the use of this character as an indicator of different origins. Again, the tangentially and radially orientated

* R. R. Gates in Bot. Gaz. xliii. (1907) 81–114.
‡ R. R. Gates in Arch. f. Zell. iii. (1909) 525–552.
† Anna M. Lutz, Science, xxvi. (1907) 151.
§ F. Keeble in Journ. Gen. ii. (1912) 163.

ovule, as exemplified by *Cornus* and *Helwingia* respectively, may prove a useful character, the sympathetic development of the ovary in relation to the form of ovule having evidently evolved independently in each genus during the period of abortion through which the ovary has conceivably passed.

Phylogeny of the Hamamelidaceæ.—Robert Brown * considered that the Hamamelidaceæ possessed affinities with Bruniaceæ on the one hand and the Cornaceæ on the other. Affinity with the Bruniaceæ and Saxifragaceæ is more nearly consistent with well-balanced modern opinion.

Lindley † placed *Altingia* and *Liquidambar* between the Betulaceæ and Salicaceæ. Hallier ‡, in 1905, reverts to this affinity, conceiving the descent of the Betulaceæ from the Hamamelidaceæ. This plausible supposition is not supported by the embryology, and the endosperm as a crucial character has been too lightly regarded. L. S. Gibbs § suggests that the Alsinoideæ illustrate an intermediate stage in the development of the exalbuminous seed by a progressive reduction in the functions of the nucellus; and Péchoutre's ‖ investigations point to a similar tendency in the Rosaceæ. But even if the evolution of the exalbuminous seed has occurred in several families, it scarcely follows, especially when the embryology is different, that the Betulaceæ are virtually exalbuminous Hamamelidoideæ. The families are probably convergent, with separate and distinct lines of origin.

The Hamamelidaceæ, whilst exhibiting diverse characters of floral organization, form nevertheless a fairly homogeneous group. It is difficult to subdivide the family into well-defined sections, and every criterion hitherto used has failed. The characters are in harmony with Saxifragacean characteristics, and the Hamamelidaceæ pass presumably into a pro-Saxifragacean plexus forming an older line originating perhaps from more than one progenitor.

Phylogeny of the Caprifoliaceæ.—The Caprifoliaceæ are remarkable, owing to a singular correspondence in several important and deep-seated characters—the epigynous ovary, the biseriate ovules, the evolution of an axially suspended seed owing to abortion, and the tangentially orientated and similarly organized ovule. Here, again, the characters that have been adopted to separate the genera into groups or even families have proved futile, except in the case of *Adoxa*.

Diervilla temptingly recalls *Polyosma*, but the resemblance reveals divergencies from the Caprifoliaceæ rather than a possible prototype; the differences, however, are not incompatible with affinity on the Saxifragacean side.

Lindley ¶ suggested a possible connection between *Sambucus* and *Hydrangea*, partly

* Robert Brown, 'Characters and Descriptions of Three new Species of Plants' (London, 1818).

† J. Lindley, Veg. King. 2nd ed. (1847) 253.

‡ Hans Hallier in New Phyt. iv. (1905) 151.

§ L. S. Gibbs in Ann. Bot. xxi. (1907) 51.

‖ F. Péchoutre in Ann. Sci. Nat., Bot. 8me sér. xvi. (1902) 156.

¶ J. Lindley, Veg. King. 767.

influenced by the sterile ray-florets in both genera. Here, although the reasons given may now be thought unsound, and the differences between the types compared are greater than in the former case, a second reasonable line of descent on the Saxifragacean side may be contemplated.

The organization of the ovary of *Leycesteria* is not far removed from that of *Pyrus*, whilst biseriate ovules are found in *Spiræa*, but the structure of the ovule is not compatible with direct descent on the Rosacean side. *Leycesteria* perchance originated from an issue of the pro-Rosacean plexus, in which the ovule itself progressed and the biseriate rows, reduced in *Pyrus*, were retained.

Phylogeny of the Cornaceæ.—The Cornaceæ of both Harms and Wangerin are polyphyletic, and the family consists chiefly of outlying forms, representatives of stocks that have become obsolete.

There is no warrant from recent discoveries for the recession of *Garrya* to the vicinage of the orthotropal cohorts. *Garrya* is more reasonably linked by slender and far distant threads to the Bruniaceæ and Hamamelidaceæ.

Aucuba is probably a scion from pro-Rosacean stock. Here the descending form of ovule found in *Pyrus* and *Prunus* has become specialized, and the ovary considerably reduced.

It is curious that, whilst this morphological analysis dissociates *Garrya* and *Aucuba*, the most successful reciprocal effects in cross-grafting have been obtained with these genera. Owing to the kindness of Sir Harry Veitch, the private records of a long series of experiments, records of successes and failures in cross-grafting, have been placed at the writer's disposal. Here, whilst the successful grafts are nearly always between genera of the same family, it must be admitted that failures between nearly related genera are numerous. In one case alone a graft succeeded, and that only for a time, in which genera of different families were used—the reciprocal grafting of *Ilex Perneyii* and *Buxus balearica*. But genera from different families were infrequently chosen for experiment. The following reciprocal grafts failed:—*Cornus* and *Aucuba*, *Griselinia* and *Aucuba*, *Sambucus* and *Viburnum*, *Loropetalum* and *Hamamelis*, *Distylium* and *Sycopsis*, *Nyssa* and *Aucuba*, *Aralia* and *Hedera*.

Helwingia is difficult to relate. It may be, perhaps, regarded as an epigynous representative of a parallel line to the Sapindaceæ.

Davidia and *Nyssa* are isolated forms abutting on the Araliaceæ, but scions from different progenitors belonging to a pro-Araliacean stock. Here obtains a specialized form of the Rosacean ascending ovule; so that this plexus might extend through issues now extinct into the primitive Rosaceæ.

Alangiaceæ still await a keen scrutiny of the ovule, and leave the respective claims of the Cornaceæ, Combretaceæ, and *Polyosma* unsatisfied. *Alangium* appears to be a reduced analogue of *Davidia*, possessing the Cornean type of ovule.

Corokia and *Griselinia* are provisionally regarded as outlying forms to *Cornus* that have had an independent origin.

Vascular Structure of the Flower in Angiosperms.—Since Van Tieghem's * memoir of 1868, when the vascular systems of several evolutionary types of both monocotyledonous and dicotyledonous flowers were examined, this subject has progressed very little beyond the purely descriptive stage. Hence the leading features of economical advance may be outlined here. The simplest trace of a single carpel consists of a median or dorsal and two marginal or ventral bundles. In the Hellebore, where the carpels are united at their bases, bivalent traces occur in the basal portion. Pronounced cases of syncarpy reveal two series of bundles in the ovary-wall—the outer homologous with dorsal, the inner with marginal bundles, and in *Geranium longipes* the marginal bundles coalesce in pairs. The vascular changes which supervene with perigyny and epigyny vary in different families. In *Aralia* the stemonal and perianthic traces, now included in the ovary-wall, form a third and outermost series of bundles. The two outer series, distinct in *Aralia*, have become synthesized to form one in *Castanea*, several genera of Cornaceæ, and the epigynous Sympetalæ. The amalgamation is incomplete in *Davidia* and *Marlea*. Another mode of origin of the single outer series is indicated in the Hamamelidaceæ, where the single series of bundles, evident as far as the insertion of the perigynous ridge, might have a further upward extension as the ovary becomes inferior.

The last traces of the dorsal carpellary bundles may disappear, as in *Lonicera* and *Leycesteria*, but here the bundles passing to stamens and petals are perhaps not strictly homologous with stemonal and petal traces respectively.

By a further economical advance the bundles in the single series, which in *Cornus*, *Leycesteria*, and many other genera are equal to the sum of the petals and stamens, are in *Viburnum*, the Campanulaceæ, and Compositæ reduced to one-half the number.

Lines of asymmetrical development are exemplified by *Viburnum*, a precursor of the irregular vascular systems which prevail in the Valerianaceæ.

No phylogenetic significance can be attached to a particular form of vascular system; but vascular details may afford a clue in support of an interpretation of origin, as in *Viburnum*, *Aucuba*, etc., but they should always be used with the utmost reserve.

The Ovule in Angiosperms.—Mirbel † wrote in 1829: "On peut dire qu'à cette première époque tous les ovules sont orthotropes."

The orthotropous ovule is primitive to the anatropous types.

The ovule, in *Juglans regia*, according to Benson and Welsford ‡, is not strictly orthotropous, but exhibits "one mode of the phylogenetic origin of the orthotropous basal ovule from an anatropous parietal type." Benson and Welsford describe two types of flower: in one there are two opposite basal parietal placentæ, of which one bears a single erect ovule and the other is barren; in the other, the ovule is apparently borne by the two placentæ and becomes basal and orthotropous. Now, in the first case, the

* Ph. Van Tieghem in Ann. Sci. Nat., Bot. 5me ser. ix. (1868) 127-226, t. 9–12.

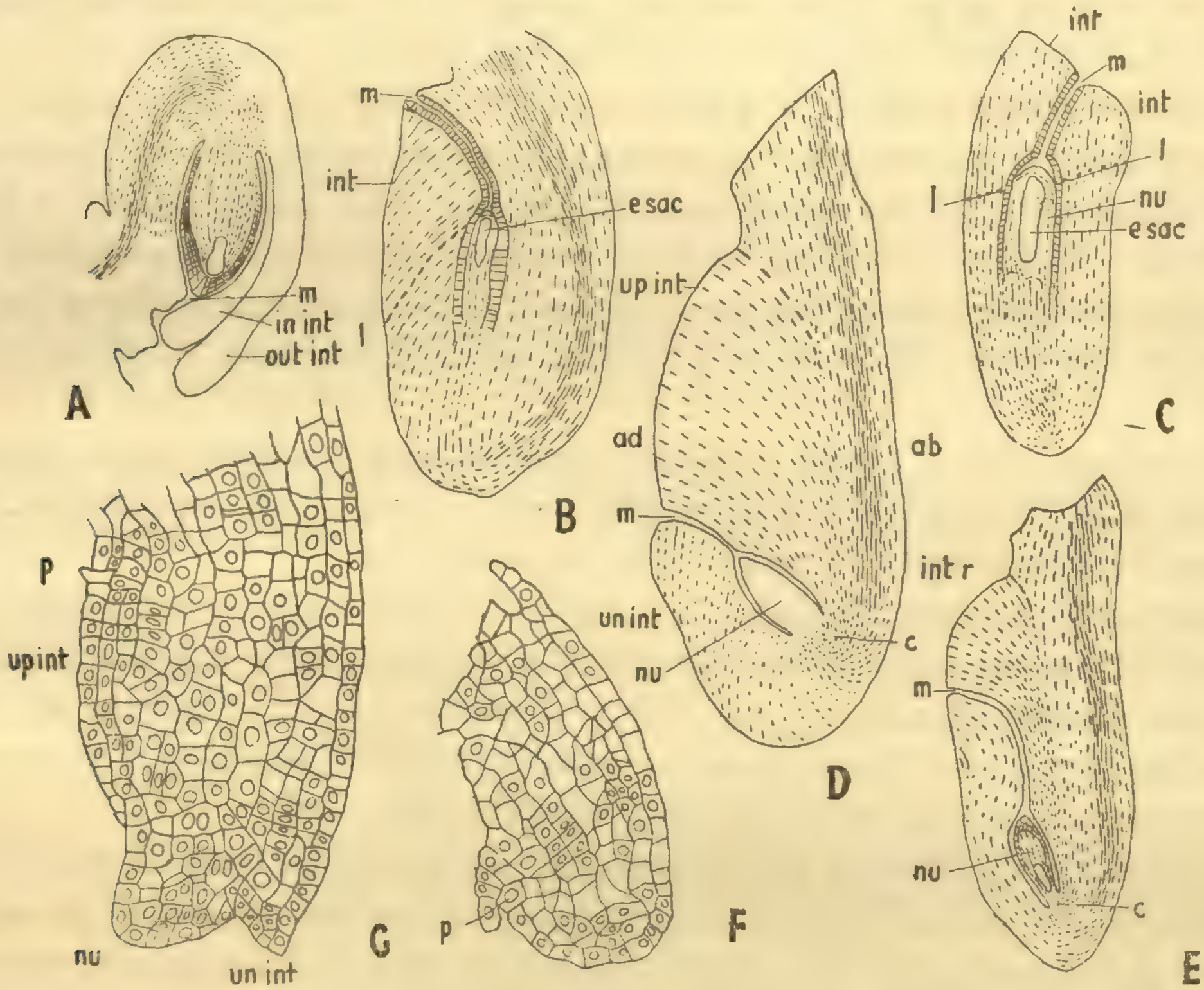
† Mirbel in Mém. de l'Acad. des Sciences, ix. (1830) 611.

‡ Benson and Welsford in Ann. Bot. xxiii. (1909) 629.

ovule, being erect, is only slightly anatropous and hence can be regarded as exhibiting the very earliest stage in the evolution of the anatropous ovule.

The stage in evolution evident in *Juglans* is followed by the complete inversion of the nucellus, owing to the curvature of the raphe as in the Cactaceæ and Saxifragaceæ, and further by the congenital union of the raphe and integument as exemplified by the Rosaceæ. This phase of evolutionary advance is characterized by the separation of several anatropal types. Two types obtain in the Rosaceæ: one "ascending," with the nucellus directed upwards as in *Cerasus juliana*; the other, "descending," with the

Text-fig. 13.



Diagrams illustrating the structure of the ovule.

A, *Pyrus Malus*; B, *Helwingia ruscifolia*; C, *Davidia involucrata*; D–G, *Aucuba japonica*.

ad=adplacental side; *ab*=abplacental side; *c*=chalaza; *e.sac*=embryo-sac; *int*=integument; *int.r*=cell-rows of integument; *in.int*=inner integument; *out.int*=outer integument; *up.int*=upper margin of integument: *un.int*=lower margin of integument; *l*=limit of integument; *m*=micropyle; *n*=nucellus; *p*=pivot cell.

nucellus directed downwards, as in *Cratægus Oxyacantha* and *Pyrus Malus* (Text-fig. 13, A). The former type is not far removed from the "dorsal" ovule which prevails throughout whole families, such as the Araliaceæ, whilst the ventral ovule in Cornaceæ (Text-fig. 13, E, *Aucuba*; B, *Helwingia*) is conceivably an advance upon the "descending" type. Specialized forms of the "dorsal" and "ventral" ovule are found in *Davidia* and *Helwingia* respectively (Text-fig. 13, C and B), where the integument (*int*) exists as a separate organ for only a short distance below the summit of the nucellus —to the line marked *l* in the figures.

The line of anatropal advance and specialization is accompanied by the transition from the bi- to the uni-tegumentary condition.

Benson *, in 1894, found all stages from two completely free integuments in Fagaceæ, to two more or less fused in Casuarinaceæ and Corylaceæ. Péchoutre †, in 1902, demonstrated a similar series in Rosaceæ and both the uni- and bi-tegumentary condition in one genus, *Spiræa*.

A third series occurs in the Ranunculaceæ, whilst one or two integuments characterizes the Dilleniaceæ and Ochnaceæ. A single integument is found, for example, in the Triuridales, Ceratophyllaceæ, Empetraceæ, Aquifoliaceæ, Cochlospermaccæ, Loasaceæ, Umbellifloræ, and prevails almost exclusively in nearly all the cohorts of the Sympetalæ.

A third line of advance lies in the direction of the reduction in bulk of the nucellus. The axile rows are numerous in the Rosaceæ, few in the Araliaceæ, and reach their minimum development in *Lilium*, *Helwingia*, and *Inula*.

Ovular Connections.—Where each loculus contains several series of ovules, as in the Saxifragaceæ, the main placental bundles branch repeatedly throughout their course on their outer side; branches of the second and third order arise from these and the ultimate branchlets supply the ovules—one to each. Transitional vascular stages, accompanying the change from the multiseriate to the biseriate arrangement, have not been studied; but when the ovules are in two series, as in *Leycesteria*, the system is reduced, each main bivalent axial bundle produces short branches on either side, supplying ovules in the right- and left-hand loculus respectively—one branch to each ovule. When the ovules in the double series are reduced to a terminal pair, rendering each loculus biovulate, the branches are also reduced to two as in *Aralia* and the Hamamelidaceæ. The further change from the biovulate to the uniovulate loculus involves several instances. Thus the change from *Aralia* or *Corylopsis*, where one of a pair of ovules is sterile, to *Hamamelis*, where one placenta of each pair is barren, is accompanied by the abortion of the branch pertaining to the barren placenta and the ovule receives a single bundle. But where the single ovule is axially borne, the ovular trace is frequently double, receiving a vascular supply equivalent to that of a pair of axially borne ovules. In *Davidia*, the branches uniting to form the ovular trace arise from several small bundles extending in the right- and left-hand septa and pertain to the right- and left-hand sides of the carpel; in *Cornus*, the branches arise from bivalent peripheral bundles; and in *Helwingia*, where the median branch from an axial bundle forms the ovular trace, the axial bundle represents two united marginal bundles of the same carpel, so that the median branch may be considered bivalent.

In more advanced stages of reduction, where the septa disappear and the ovary becomes uniovulate, various anomalies occur, such as have been described in detail for *Viburnum*, *Corokia*, *Griselinia*, and *Nyssa*.

It is highly probable that a parallel series of stages will be found leading towards

* M. Benson in Trans. Linn. Soc., Bot. 2nd ser. iii. (1894) 409–424, t. 67–72.

† F. Péchoutre in Ann. Sci. Nat., Bot. 8me sér. xvi. (1902) 88.

genera where the ovule in the uniovulate loculus or ovary is basal. In the case of *Juglans regia*, already cited, the ovule, when parietally borne, is supplied by the bundle in the corresponding placenta, as in *Aralia*; but when basal (axially situated), bundles from both placentæ are contributory as in *Cornus*.

Ovular Vascular System.—Integumentary vascular tissue has been known since 1829, when Mirbel * described and figured the vascular systems of the ovules of *Myrica pensylvanica*, *Corylus Avellana*, *Juglans regia*, and *Quercus Robur*, and states:—"On voit fréquemment à la superficie de la Primine des nervures tantôt simples tantôt ramifiées qui partent de la chalaze et se dirigent vers l'Exostome." A. Gris †, in 1861, figured integumentary bundles in *Ricinus communis*; Van Tieghem ‡, in 1872, indicates several examples selected from different families, and Le Monnier §, in the same year, described and figured the nervation in many seeds. The vascular system in *Myrica*, *Juglans*, and certain Amentiferæ was rediscovered by E. M. Kershaw ‖ in 1909.

Balfour ¶ suggested that in non-vascular seeds the integument forms the water-supply of the ovule.

L. S. Gibbs ** subsequently showed that the outer integument in the Alsinoideæ actually performs this function.

The writer †† explained that in *Davidia* the ovular bundle branches and forms a considerable system in the young seed, and the "integument" with its vascular system is organized as an elaborate reservoir during the accumulation of an abundant endosperm.

The water problem has to be solved in connection with seed-development from ovules of numerous types, and it is clear that a similar device is adopted time and again in phylogeny, early or late in ovular development according to special needs. Hence the possession of a vascular supply is scarcely of considerable phylogenetic importance, as suggested by E. M. Kershaw.

Phylogeny of Angiosperms.—The author of each great system has in turn realized that his classification is far from perfect and contains speculative groups difficult to define. Hence the finding that two families of Angiosperms are polyphyletic, in itself, merely corrects or modifies a fragment of Engler's system, and, indeed, Engler has already recognized the polyphyletic nature of his original Cornaceæ by adopting Wangerin's not satisfactorily established arrangement in 'Das Pflanzenreich.' But the facts that have influenced the writer to deduce polyphyletic origin for these families are derived from an investigation in detail as yet unattempted, except perhaps in the

* Mirbel in Mém. de l'Acad. des Sciences, ix. (1830) 632.

† A. Gris in Ann. Sci. Nat., Bot. 4me sér. xv. (1861) 5–9, t. 2.

‡ Ph. van Tieghem in Ann. Sci. Nat., Bot. 5me sér. xvi. (1872) 228–232.

§ G. Le Monnier in Ann. Sci. Nat., Bot. 5me sér. xvi. (1872) 233–305, t. 9–12.

‖ E. M. Kershaw in Ann. Bot. xviii. (1909) 353, 692.

¶ I. B. Balfour in Proc. Brit, Assoc. Adv. Sci., Bot. Sect. (1901).

** L. S. Gibbs in Ann. Bot. xxi. (1907) 25–55, t. 5, 6.

†† A. S. Horne in Trans. Linn. Soc., 2nd ser. Bot, vii. (1909) 315.

case of very few families, and he claims polyphyly for at least three genera of the Caprifoliaceæ and eight of the Cornaceæ, although in the latter family some genera have remained closely associated for a considerable period. Now very many families comprise a certain number of obscure forms, and subsequent analysis may determine not only that these cannot be included in any existing family, being the sole representatives of extinct lines, but even the apparently stable members of the family may show evidence of parallel development and convergence.

Allowance must also be made in phylogenetic systems for cases where differently organized forms may possess probable affinity, such as, for instance, *Polyosma* and *Diervilla*, but the suggested origin of one from the other must be compatible in all respects with morphological structure and evolutionary methods established by experiment; thus, relatives of *Polyosma* should possess the power of advance towards the condition in *Diervilla*, both with respect to gamopetaly and the number and nature of the ovules.

It is a long-established custom to regard certain characters as more constant and dependable than others, conceiving that the ovule, for example, would be less liable to change than more superficial characters. According to De Vries's view of indiscriminate mutation, however, the ovule would be equally liable to change, but since mutation is a rare phenomenon, difficult to perceive. Even then, however, the ovule would pass through relatively fewer mutations than the floral organization, so that a certain form of ovule might remain constant for a considerable range of floral and vegetative change. Hallier reverts to an indiscriminate use of characters without due regard to relative value; thus *Garrya* is retained in the Cornaceæ owing to the discovery of aucubin by Hérissey and Lebas * in this genus, although a criterion of this kind is of doubtful value unless supported by considerable research. Hallier † has attempted that which cannot be accomplished from the evidence yet accumulated, and the inevitable result of this finds expression in the extreme instability of his system.

Knowledge of the phylogeny of Angiosperms can only be truly advanced by the detailed morphological and experimental investigation of many more families, and then, but not till then, can Engler's system be replaced by a greater scheme more nearly approximating to natural relationships. In such a scheme the barrier between the Polypetalæ and Sympetalæ will doubtless be removed, and the various families, upon reconstruction, will be arranged in plexuses according to their probable origin and relationship. It is possible to forecast the lines upon which this will be attempted, but the effort lies beyond the scope of this present work.

I desire to acknowledge my indebtedness to Mr. C. E. Jones, B.Sc., F.L.S., for many friendly suggestions; to Dr. A. B. Rendle, F.R.S., for valuable help and criticism; and, lastly, to Professor J. B. Farmer, F.R.S., for his continuous advice and encouragement throughout the investigation.

* Hérissey and Lebas in Bot. Centralbl. cxvii. (1911) 176.

† H. Hallier in Beihefte Bot. Centralbl. xxiii. 2 (1908) 81, and Arch. Néerl. d. Sci. Ex. et Nat. sér. 3, Bd. i. 146 (1912).

Bibliography.

1. Arber, E. A. Newell.—Synanthy in *Lonicera*. Journ. Linn. Soc., Bot. xxxv. (1903) 463–474.
2. Aubert, M. P. L.—Organogénie de la fleur dans le genre *Salix*. Adansonia, xi. (1873–76) 183–186, t. 10.
3. Baillon, H.—Observations sur les Saxifragacées. Adansonia, v. (1864–65) 282–304; vi. (1865–66) 1–15.
4. —— Recherches sur l'*Aucuba*. *Ib.*, v. (1864) 179–203.
5. —— Traité du développement de la fleur et du fruit. VII. Corylées. *Ib.*, xi. (1874) 163–174. X. Castaneacées. *Ib.*, xii. (1876–79) 1–20. XII. Garryacées. *Ib.*, 264–269.
6. —— Sur deux nouveaux genres apétales. *Ib.*, x. (1871–73) 112–117.
7. —— Sur les affinités des *Helwingia*. Bull. Soc. Linn. Paris, i. (Nov. 1877) 137–139.
8. —— Sur l'organogénie florale et la graine des *Garrya*. *L. c.*, i. (Nov. 1877) 139–141.
9. —— Histoire des Plantes. Paris. Hamamelideæ, iii. 456–461 (1871–2); Combretaceæ, vi. 277–283 (1877); Cornaceæ et Umbelliferæ, vii. 79–83 (1879).
10. —— Natural History of Plants. (Trans. by Hartog.) 1871 *etc.*
11. —— Nouvelles notes sur les Hamamélidées. Adansonia, x. 120–137 (1871–73).
12. —— Plantes de Madagascar, Atlas, iii. (1896).
13. Baker, J. G.—Further Contributions to the Flora of Central Madagascar. Journ. Linn. Soc., Bot. xxi. (1884–85) 317–353, 407–455.
14. —— *Melanophylla crenata*. Hook. Ic. Pl. xxv. (1896) t. 2499.
15. Bateson, W.—Mendel's Principles of Heredity. London, 1913. 8vo.
16. Bateson, W., Miss E. R. Saunders, and R. C. Punnett.—Experimental Studies in the Physiology of Heredity. Reports to the Evolution Com. Roy. Soc. ii. (1905); iii. (1908).
17. Benson, Margaret J.—Contributions to the Embryology of the Amentiferæ. Part I. Trans. Linn. Soc., 2nd ser. Bot. iii. (1894) 409–424, t. 67–72.
18. Benson, Margaret J., Elizabeth Sanday, and Emily Berridge.—Contributions to the Embryology of the Amentiferæ. Part II. Trans. Linn. Soc., 2nd ser. Bot. vii. (1906) 37–44, t. 6.
19. Benson, Margaret J., and Evelyn J. Welsford.—The Morphology of the Ovule and Female Flower of *Juglans regia* and of a few allied genera. Ann. Bot. xxiii. (Oct. 1909) 623–633.
20. Bentham, G.—Plantæ Hartwegianæ. Londini, 1839–57. 8vo.
21. Bentham, G., et J. D. Hooker.—Genera Plantarum. i. (Hamamelidaceæ), 664–669; (Cornaceæ) *l. c.*, 947–952; ii. (Caprifoliaceæ) 1–7.
22. Bessey, Ernst A.—The Comparative Morphology of the Pistils of the Ranunculaceæ, Alismaceæ, and Rosaceæ. Bot. Gazette, xxvi. (1898) 297–312, t. 25.
23. Billings, F. H.—Beiträge zur Kenntniss der Samenentwicklung. Flora, lxxxix. (1901) (Caprifoliaceæ, p. 303).
24. Blume, C. L.—Museum Botanicum Lugduno-Batavum, i. (1849–1851).
25. Boerlage, J. G.—Flora van Nederlandsch Indie, i. Polypetalæ (1890).
26. Brown, Robert.—Observations on the Natural Family of the Plants called Compositæ. Trans. Linn. Soc. xii. (1817) 76–142.
27. —— Characters and Descriptions of three new species of Plants (1818). Miscell. Bot. Works of R. B. vol. ii. (1867) 319–328.
28. Campbell, D. H.—Entwicklung des Embryosackes von *Peperomia pellucida*. Ber. Deutsch. Bot. Gesell. xvii. (1899) 452–456, t. 31.
29. —— A peculiar Embryo-sac in *Peperomia pellucida*. Ann. of Bot. xiii. (1899) 626.
30. Candolle, A. de.—Prodromus. Helwingiaceæ, xvi. ii. 680–681 (1868).

31. Carrière, E. A.—Revue Horticole, 1869, 17–18.
32. —— „ „ 1879, 154–155.
33. Clarke, Benjamin.—On the Structure of the Ovary of *Marlea* and Affinities of Alangieæ. Hooker's Kew Journal of Botany, vol. ii. (1850) 129–135, t. 5.
34. Clarke, C. B.—Oleaceæ. Hooker's Flora of British India, iii. 590–618.
35. Clements, Frederick Edward.—Research Methods in Ecology. Lincoln, Nebr., 1905.
36. Coulter, J. M., and W. H. Evans.—A Revision of the N. American Cornaceæ. Bot. Gazette, xv. (1930) 30–38, 86–97.
37. Coulter, J. M.—Contribution to the Life History of *Ranunculus*. Bot. Gazette, xxv. (1898) 73–86, t. 4–7.
38. Darwin, Charles Robert.—Animals and Plants under Domestication. London, 1868. 2 vols., 8vo. 2nd ed. revised (1893).
39. Decaisne, J.—Remarque sur les affinités du genre *Helwingia*, et établissement de la famille des Helwingiacées. Ann. Sci. Nat. Bot. 2me sér. vi. (1836) 65–76.
40. Decaisne, J., et E. Le Maout.—Traité Générale de Botanique. Paris, 1868. 4to.
41. —— A General System of Botany (trans. by Mrs. Hooker). London, 1873. 4to.
42. Digby, L.—The Chromosomes of the Hybrid *Primula kewensis*. Proc. Brit. Assoc. Adv. Sci. Portsmouth, 1911 (1912), 585–586.
43. Ducamp, L.—Recherches sur l'embryogénie des Araliacées. Ann. Sci. Nat., Bot. 8e sér. xv. (1902) 311–402, t. 6–13.
44. Eichler, A. W.—Blütendiagramme. Leipzig, 1875–78. 2 vols., 8vo.
45. Endlicher, S.—Corneæ, Genera Plantarum (1839) 798–799; Suppl. v. (1850) 17: Hamamelideæ, Gen. Pl. (1839) 803–805: Lonicereæ, Gen. Pl. (1839) 566–570.
46. Engler, A.—Syllabus der Pflanzenfamilien. Ed. vii. Berlin (1912).
47. Engler, A., and K. Prantl.—Die Natürlichen Pflanzenfamilien. Araliaceæ, *see* Harms; Caprifoliaceæ, *see* Fritsch; Cornaceæ, *see* Harms; Hamamelidaceæ, *see* Niedenzu.
48. Farmer, J. B.—On the Development of the Endocarp of *Sambucus nigra*. Ann. of Bot. ii. (1889) 389–392.
49. Fritsch, Carl.—Caprifoliaceæ. Engl. u. Prantl, Nat. Pflanzenf., Teil iv. Abt. 4, 156–169 (1891).
50. —— Verhandl. d. Zool.-bot. Ges. in Wien, xlii. (1892) 7–10.
51. Gibbs, Lilian Suzette.—Notes on the Development and Structure of the Seed in the Alsinoideæ. Ann. Bot. xxi. (1907) 25–55, t. 5, 6.
52. Goebel, Carl.—Organography of Plants. Transl. by Balfour: Oxford, 1904–1905. 2 vols. 8vo.
53. Grélot, Paul.—Recherches sur la nervation carpellaire chez les Gamopétales bicarpellées de Bentham and Hooker. Compt. rendus, cxxii. p. 1144 (1896); cxxv. p. 380 (1897).
54. —— Recherches sur le système libéroligneux floral des Gamopétales bicarpellées. Ann. Sci. Nat., Bot. 8e sér. v. (1897) 1–154, t. 1–8.
55. Gris, A.—Note sur le développement de la graine du Ricin. Ann. Sci. Nat. Bot. 4me sér. xv. (1861) 5–9, t. 2.
56. Guignard, Léon.—Recherches sur le sac embryonnaire des Phanérogames Angiospermes. Ann. Sci. Nat., Bot. 6me sér. xiv. (1832) 26–42, t. 3–7.
57. Hallier, Hans.—Ueber den Umfang, die Gliederung und die Verwandtschaft de Familie des Hamamelidaceen. Beihefte 2, Botanisches Centralblatt, xiv. (1903) 247–260.
58. —— Provisional Scheme of the Natural (Phylogenetic) System of Flowering Plants. New Phyt. iv. No. 7 (1905) 151–162.
59. —— Neue Beiträge zur Stammesgeschichte der Dicotyledonen. Beihefte, Botanisches Centralblatt, xxiii. 2. (1908) 81–265.
60. —— Arch. Néerl. d. Sci. Ex. & Nat., Sér. iii. i. (1912) 146.

61. Harms, Hermann.—Ueber die Blüthenverhältnisse der Gattung *Garrya*. Ber. Deutsch. Bot. Gesell. Band xv. (1897) 19–21.
62. —— Die Gattungen der Cornaceen. Ber. Deutsch. Bot. Gesell. Band xv. (1897) 21–29.
63. —— Araliaceæ, Cornaceæ. Engl. u. Prantl, Nat. Pflanzenf., Teil iii. Abt. 8, 1–62 (1894) 250–270 (1898).
64. Höck, F.—Zur systematischen Stellung von *Sambucus*. Botanisches Centralbl. li. (1892) 233–234.
65. Hofmeister, W.—Embryobildung des Phanerogamen :—Caprifoliaceen. Pringsh. Jahrb. i. (1858) 120–121.
66. —— Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen. Abhandl. Königl.-Sächs. Gesell. Wiss. (1859) 533–672, t. 1–27.
67. Hooker, J. D.—Flora Novæ Zelandiæ, i. 1853–55.
68. —— Illustrations of Himalayan Plants, t. 12 (1855).
69. Hooker, J. D., et T. Thomson.—Præcursores ad Floram Indicam : Caprifoliaceæ. Journ. Linn. Soc., Bot. ii. (1858) 163–180.
70. Horne, A. S.—The Structure and Affinities of *Davidia involucrata*, Baill. Trans. Linn. Soc. 2nd ser., Bot. vii. (1909) 303–326, t. 31–33.
71. —— The Polyphyletic Origin of Cornaceæ. Proc. Brit. Assoc. Adv. Sci., Portsmouth, 1911 (1912) 585.
72. Johnson, D. S.—On the Endosperm and Embryo of *Peperomia pellucida*. Bot. Gazette, xxx. (1900) 1–11, t. 1.
73. —— On the Development of certain Piperaceæ. Bot. Gazette, xxxiv. (1902) 321–340.
74. Kershaw, Edith May.—Note on the Relationship of the Julianaceæ. Ann. of Bot. xxiii. (1909) 336–337.
75. —— The Structure and Development of the Ovule of *Myrica Gale*. Ann. of Bot. xxiii. (1909) 353–362, t. 24.
76. —— Further observations on the Structure of the Ovules of Myricaceæ and allied groups. Ann. of Bot. xxiii. (1909) 692.
77. Kurz, Sulpiz. Journ. Asiat. Soc. xliv. ii. (1875) 201, pl. 15 (*Nyssa*).
78. Le Monnier, Georges.—Recherches sur le nervation de la Graine. Ann. Sci. Nat., Bot. 5me sér. xvi. (1872) 233–305, t. 9–12.
79. Lindley, John.—The Vegetable Kingdom. 2nd ed. (1847); 3rd ed. (1853).
80. —— *Garrya elliptica*. Edwards's Botanical Register, vii. (1835) t. 1686.
81. Lloyd, F. E.—The Comparative Embryology of the Rubiaceæ. Mem. Torrey Bot. Club, viii. (1902) 1–112.
82. Lyon, Florence May.—A Contribution to the Life History of *Euphorbia corollata*. Bot. Gazette, xxv. (1898) 418–426, t. 22–24.
83. Maximowicz, Carl Johann.—Diagnoses de Nouvelles Plantes Asiatiques. Bulletin de l'Académie Impériale des Sciences de St. Pétersbourg. *Lonicera*, xxiv. (1878) 35 ; *Viburnum*, xxvi. (1880) 474 ; *Triosteum*, xxvii. (1881) 476 ; *Abelia, Diervilla*, xxxi. (1887) 54–62.
84. Merz, M.—Untersuchungen über die Samentwickelung der Utricularieen. Flora, lxxxiii. (1897) 77–87, t. 3.
85. Mirbel, C. F. Brisseau.—Nouvelles recherches sur la structure et le développement de l'Ovule végétal (1828). Mém. de l'Acad. des Sciences, ix. (1830) 609–629.
86. —— Addition aux nouvelles recherches sur la structure et les développements de l'Ovule (1829). Mém. de l'Acad. des Sciences, ix. (1830) 629–684.
87. Niedenzu, Franz.—Hamamelidaceæ. Engl. u. Prantl, Nat. Pflanzenf., Teil iii. Abt. 2 a. (1891) 115–130.

88. Oersted, Anders S.—Til Belysning af Slaegten *Viburnum*. Vidensk. Meddel. Naturh. Foren. Kiobenh. 1860 (1861) 267–305, t. 7, 8.

89. Oliver, Daniel.—*Sycopsis*, a new genus of Hamamelidaceæ. Trans. Linn. Soc., xxiii. (1860) 83–89, t. 8.

90. —— Note on *Hamamelis* and *Loropetalum* ; with a description of a new *Anisophyllea* from Malacca. *L. c.* (1862) 457–461, t. 48.

91. —— *Nyssa sinensis*. Hooker's Ic. Pl. t. 1964 (1891).

92. —— *Davidia involucrata*. *L. c.* t. 1961 (1891).

93. Oliver, Frank Wall.—On the Structure, Development, and Affinities of *Trapella*, a new genus of Pedalineæ. Ann. of Bot. ii. (1888) 75–115.

94. Palacký, J.—Plantarum Madagascariensium. Fasc. iv. (1906).

95. Payer, J. B.—Leçons sur les Familles naturelles des Plantes (1860–1865) 124.

96. —— Organogénie de la Famille des [Ombellifères]. Ann. Sci. Nat., Bot. 3e sér. xx. (1853) 111–118, t. 14.

97. —— Traité d'Organogénie comparée de la Fleur. Paris, 1857. 2 vols., 8vo.

98. Péchoutre, F.—Développement de l'ovule et de la graine des Rosacées. Ann. Sci. Nat., Bot. 8me sér. xvi. (1902) 1–158.

99. Sargent, C. S.—Silva of N. America : v. (Hamamelidaceæ to Sapotaceæ). Boston & New York, 1893. 8vo.

100. Schnegg, H.—Beiträge zur Kenntnis der Gattung *Gunnera*. Flora, xc. (1902) 161–208.

101. Sertorius, Adolf.—Beiträge zur Kenntnis der Anatomie der Cornaceæ. Diss., München, 1893 ; in Bull. de l'Herbier Boissier, i. (1893) 469–484, 496–512, 551–570, 614–639.

102. Shoemaker, D. N.—On the Development of *Hamamelis virginiana*. Bot. Gazette, xxxix. (1905) 248–266.

103. Tanfani, C.—Morfologia ed istologia del frutto e del seme delle Apiaceæ. Nuove Giorn. Bot. Ital. xxiii. (1891) 451–469, t. 4–7.

104. Thunberg, C. P.—Flora Japonica, pp. 4 & 64, tab. 12 & 13 (1784).

105. Tognini, F.—Ricerche di morfologie ed anatomia sul flore feminille e sul frutto del Castagno. Atti del R. Ist. Bot. dell' Univ. di Pavia (1892) (Estr. pp. 35, tt. 3).

106. Van Tieghem Ph. E. L.—Recherches sur la structure du Pistil. Ann. Sci. Nat., Bot. 5me sér. ix. (1868) 127–226, t. 9–12.

107. —— Note sur les divers modes de nervation de l'ovule et de la graine. Ann. Sci. Nat., Bot. 5me sér. xvi. (1872) 228–232.

108. —— Structure de quelques ovules et parti qu'on en peut tirer pour améliorer la Classification. Journ. de Bot. xii. (1898) 198–220.

109. —— Traité de Botanique. Paris, 1884, 2 vols., 8vo. ; 2me éd., *ib.*, 1886–1891, 2 vols., 8vo.

110. Vesque, J.—Développement du sac embryonnaire des Phanérogames Angiospermes. Ann. Sci. Nat., Bot. 6me sér. vi. (1878) 237–285, t. 11–16.

111. —— Nouvelles recherches sur le développement du sac embryonnaire des Phanérogames Angiospermes. *L. c.* viii. (1879) 261–390, t. 12–21.

112. Vidal, Louis.—Sur la structure et le développement du pistil et du fruit des Caprifoliacées. Bull. Soc. de Statistique, Grenoble, 4me sér. t. iv. (1899) 157.

113. —— La course des faisceaux dans le receptacle floral des Labiées. Journ. de Bot. xii. (1898) 46–52.

114. Vries, Hugo de.—The Mutation Theory ; transl. by J. B. Farmer and A. D. Darbishire. London, 1910–11. 2 vols., 8vo.

115. Walpers, W. G.—Annales Botanices Systematicæ. (Hamamelidaceæ) ii. 272–276 (1851–52) ; (Loniceræ) *ib.* 732–733 ; (Cornicæ) *ib.* 725 ; (Hamamelidaceæ) iii. 842 (1853).

116. Wangerin, W.—Garryaceæ, Nyssaceæ, Alangiaceæ, and Cornaceæ, in Engler's Das Pflanzenreich, Heft 41 (Leipzig, 1910).
117. —— Die Umgrenzung und Gliederung der Cornaceæ. Engl. Bot. Jahrb. xxxviii. (1906), Beibl. n. 86.
118. Warming, E. J. B.—De l'Ovule. Ann. Sci. Nat., Bot. 6me sér. v. (1877) 177–266, t. 7–13.
119. Webb, J. E.—Morphological study of Flowers of *Spiræa*. Bot. Gazette, xxxiii. (1902) 451–460.
120. Wettstein, R. von.—Handbuch der systematischen Botanik, i. & ii. (1901–08).
121. Wittrock, V. B. Om *Linnæa borealis*: En jemnförande biologisk, morfologisk och anatomisk undersökning. Botaniska Notiser, Lund, (1878) 17–32, 49–54, 83–96, 122–127; (1879) 9–20, 137–150.
122. —— *Linnæa borealis*, L.: Species polymorpha et polychroma. Act. Hort. Bergiani, iv. n. vii. (1907) pp. 187, tt. 13.

EXPLANATION OF THE PLATES.

Plate 28.

Fig. 1. *Cornus Amomum*. Young flower.
Fig. 2. *C. Amomum*. Young flower with two petals removed.
Fig. 3. *C. alba*. Fruit.
Fig. 4. *Marlea platanifolia*. Portion of a very young inflorescence with flowers in a stage prior to the development of the ovarian cavity.
Fig. 5. *M. platanifolia*. Single flower older than 4, ovary still undeveloped.
Fig. 6. *M. platanifolia*. Portion of a flower slightly older than 5.
Fig. 7. *M. platanifolia*. Flower slightly older than 6, with some of the petals and stamens removed.
Fig. 8. *Aucuba himalaica*. Normal flower.
Fig. 9. *A. himalaica*. Flower with six petals.
Fig. 10. *A. himalaica*. Flower with five petals and one stamen.
Fig. 11. *A. himalaica*. Flowers with petals removed showing bilobed style.
Fig. 12. *A. himalaica*. Flower with petals removed showing three styles.
Fig. 13. *Garrya elliptica*. Female catkin, nat. size.
Fig. 14. *G. elliptica*. Female flower with one style bilobed.
Fig. 15. *G. elliptica*. Young fruit slightly enlarged.
Fig. 16. *G. elliptica*. Portion of male inflorescence.
Fig. 17. *G. elliptica*. Portion of male inflorescence, bracts removed.
Fig. 18. *G. elliptica*. Single flower.
Fig. 19. *G. Thuretii*. Portion of male inflorescence, showing one "flower" with four perianth-segments and nine stamens.
Fig. 20. *G. Thuretii*. Single "flower" with seven perianth-segments and seven stamens.
Fig. 21. *G. Thuretii*. Another "flower" with five perianth-segments and ten stamens
Fig. 22. *G. laurifolia*. A terminal male flower (*br* = bract).
Fig. 23. *G. laurifolia*. The same flower, different view.
Fig. 24. *G. laurifolia*. Terminal flower.
Fig. 25. *G. laurifolia*. Lateral flower.
Fig. 26. *Helwingia ruscifolia*. Trimerous male flower.
Fig. 27. *H. ruscifolia*. Tetramerous male flower.

Fig. 28. *H. ruscifolia.* Young female inflorescence.
Fig. 29. *H. ruscifolia.* Young female flower.
Fig. 30. *H. ruscifolia.* Mature flower, pentamerous.
Fig. 31. *H. ruscifolia.* Flower with four perianth-leaves and five carpels.
Fig. 32. *H. ruscifolia.* Tetramerous flower.
Fig. 33. *Corokia Cotoneaster.* Young flower.
Fig. 34. *C. Cotoneaster.* Mature flower.
Fig. 35. *Griselinia lucida.* Young male flower.
Fig. 36. *G. lucida.* Hexamerous male flower, side view.
Fig. 37. *G. lucida.* Hexamerous male flower, viewed from above.
Fig. 38. *G. littoralis.* Male flower, closed.
Fig. 39. *G. littoralis.* Male flower, open.
Fig. 40. *G. lucida.* Very young female flower, highly magnified.
Fig. 41. *G. lucida.* An older stage.
Fig. 42. *G. lucida.* Mature flower.
Fig. 43. *G. lucida.* Fruit.
Fig. 44. *G. littoralis.* Young female flower.
Fig. 45. *G. littoralis.* Mature flower.
Fig. 46. *G. littoralis.* Young fruit.
Fig. 47. *G. littoralis.* Older fruit.
Fig. 48. *Nyssa sylvatica.* Portion of a young inflorescence.
Fig. 49. *N. sylvatica.* Young flower.
Fig. 50. *N. sylvatica.* Young flower with petals removed to show the single stamen present in this specimen.

Plate 29.

[Abbreviations:—*arch.* = archesporium; *ant.* = antipodals; *ax.* = axial row; *e. sac.* = embryo-sac; *l.* = loculus; *int.* = integument; *m.* = micropyle; *m. sp.* = megaspore; *n. ep.* = epidermis of nucellus; *par.* = parietal tissue.]

Figs. 51–54. *Symphoricarpus racemosus.* Development of sporogenous tissue in sterile ovules. 51, primary archesporial cell; 52, two sporogenous cells; 53, four sporogenous cells; 54, one of four megaspores has germinated to form an incomplete embryo-sac. ×600 approx.

Figs. 55–57. *Viburnum Lantana.* Development of the megaspores in the incomplete ovules. 55, primary archesporial cell; 56, binucleate sporogenous cell; 57, quadrinucleate sporogenous cell. ×600 approx.

Figs. 58–60. *V. Lantana.* Further development of the sporogenous tissue in the incomplete ovules. 58, portion of multinucleate protoplasmic sac showing eight of the twelve nuclei; 59, nuclei approximated in pairs; 60, segmented protoplasmic sac. ×600 approx.

Fig. 61. *Sambucus nigra.* Vertical section through a young ovule, showing single integument and nucellus with primary archesporial cell. ×290 approx.

Fig. 62. *S. nigra.* Section through an ovular rudiment showing the enlarged subepidermal cells. ×590 approx.

Figs. 63–64. *S. nigra.* The nucleus in the enlarged cells has divided to form two or four daughter nuclei. ×590 approx.

Fig. 65. *Benthamia fragifera.* Vertical section of a young ovule showing an early stage in the upgrowth of the single integument. ×290 approx.

Fig. 66. *B. fragifera.* Vertical section of a young ovule, showing the nucellus with axial rows. ×290 approx.

Fig. 67. *Cornus sanguinea.* Showing the single integument and axial rows. ×290 approx.

Fig. 68. *Aucuba japonica.* Vertical section showing the earliest stage in the development of the ovular mamelon. ×600 approx.

Fig. 69. *A. japonica.* An early stage in the formation of parietal tissue. ×590 approx.

Fig. 70. *A. japonica.* Vertical section through the nucellus showing the enlarged embryo-sac-mother-cell. ×290 approx.

Fig. 71. *A. japonica.* Transverse section of the nucellus showing two megaspores belonging to different axial rows. ×290 approx.

Fig. 72. *A. himalaica.* Reconstruction from three vertical sections of the nucellus showing a complete embryo-sac and an enlarged megaspore. ×290 approx.

Fig. 73. *Helwingia ruscifolia.* Vertical section of a young ovule showing an early stage in the development of the single integument and the nucellus. ×580 approx.

Fig. 74. *H. ruscifolia.* Vertical section of the nucellus showing the embryo-sac. ×290 approx.

Fig. 75. *Griselinia lucida.* Vertical section of the nucellus at a very early stage. ×580 approx.

Fig. 76. *G. lucida.* A slightly older stage showing axial rows. ×580 approx.

Fig. 77. *Nyssa sylvatica.* Transverse section of a very young ovule showing the nucellus invested by a single integument. ×580 approx.

N.B.—Figs. 51–77 are semi-diagrammatic.

Plate 30.

[Abbreviations:—*a*, *b*, *c*, *d*, *e*=principal bundles; *ax.*=inner peripheral bundle (corresponds to axial bundle); *in. ser.*=dorsal and lateral carpellary branches; *ov.* 1, *ov.* 2, *ov.* 3=placental branches from *ax.*; *pe.*=petal-bundle; *st.*=stemonal trace; *x*, *y*=auxiliary bundles; *x'*, *y'*=branches from *x*, *y* respectively.]

Fig. 78. Photograph of a reconstruction in wax of the vascular system of the flower of *Viburnum Lantana.* ×60 approx.

Abbreviations occurring in Text-figures 1–12.

a. Fig. 3, ovular rudiment; Fig. 4, principal bundle.
a'. Fig. 3, ovular rudiment.
ax. Figs. 2, 3, 9 and 10, axial bundles.
b. Fig. 3, ovular rudiment; Fig. 4, principal bundle.
b'. Fig. 3, ovular rudiment.
br. Fig. 4, bracteole; Fig. 11, branches from outer series.
c. Fig. 3, ovular rudiment; Fig. 4, principal bundle.
c'. Fig. 3, ovular rudiment.
d. Figs. 1, 8–10, dorsal carpellary bundle; Fig. 4, principal bundle; Fig. 5, dorsal bundle.
e. Fig. 4, principal bundle.
emb. Fig. 8, embryo.
end. Fig. 8, endosperm.
f. Fig. 8, epigynous foliole (bracteole).
in. ser. Figs. 1–12, inner series.
int. Figs. 9 and 10, integument.
l. Fig. 1, lateral carpellary bundle; Fig. 9, branches from axial bundles.

loc. Figs. 1, 5–12, loculus.

m. Fig. 1, septal or placental bundles; Fig. 8, marginal carpellary bundles.

nu. Figs. 5, 8, 9 and 12, nucellus.

o, *o′*. Figs. 5 and 6, branches concerned with ovular supply.

ob. Fig. 5, branch from *o*.

ob′. Fig. 5, branch from *o′*.

ovy. Fig. 5, inner branches ; Fig. 6, dorsal and lateral carpellary bundles.

out. ser. Figs. (etc.), outer series.

ov., *ov.* 1, *ov.* 2, etc. Figs. 2 and 3, series of ovules ; Fig. 4, placental branches from *ax* ; Fig. 10, 11, and 12, vascular tissue supplying the ovules.

pe. Fig. 1, perianth traces ; Figs. 2, 6, 7 and 10, petal bundles ; Fig. 11, petal.

pl. Figs. 1, 3, 4 and 10, placenta.

r. pe. Fig. 11, rudiments of petals.

r. st. Fig. 11, rudiments of stamens.

rud. ax. Fig. 7, rudimentary axial bundles.

se. Fig. 9, sepal bundle; Fig. 11, sepal.

st. Figs. 1, 2, 4, 10 and 12, stemonal bundles.

sty. Figs. 5, 9–12, stylar canal.

t. cy. Fig. 6, toral cylinder.

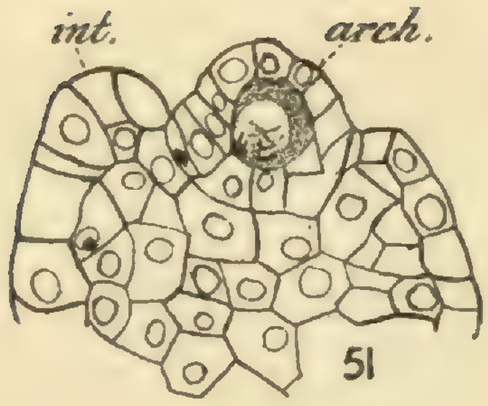
xy. Fig. 4, auxiliary bundles.

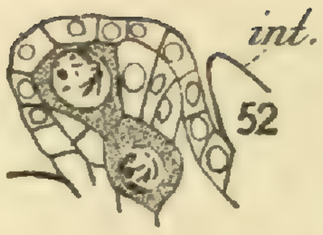
x′ y′. Fig. 4, branches from *xy*.

A. S. H. del.
J. N. Fitch lith.

West, Newman imp.

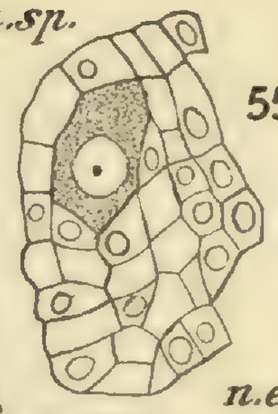
CORNACEAE.


int.
arch.
51

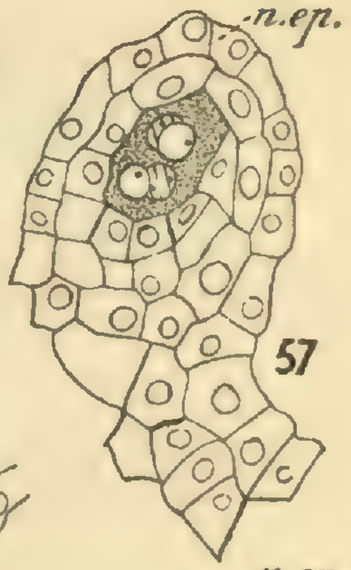

int.
52

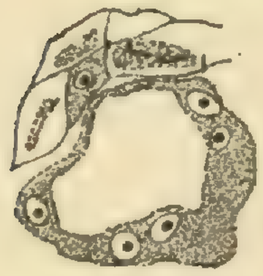
m.sp.
53

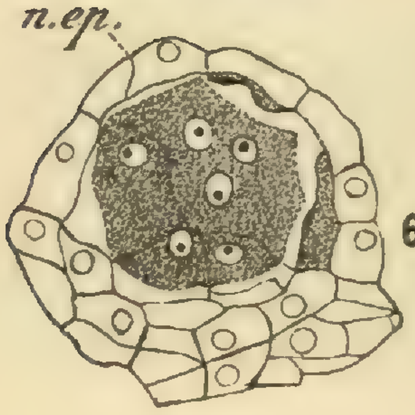
m.sp.
54
e.sac.


55

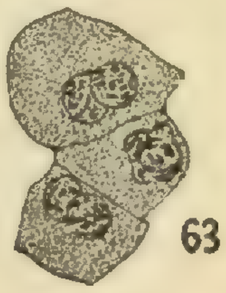
58
n.ep.

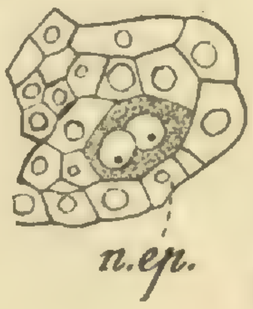

n.ep.
57

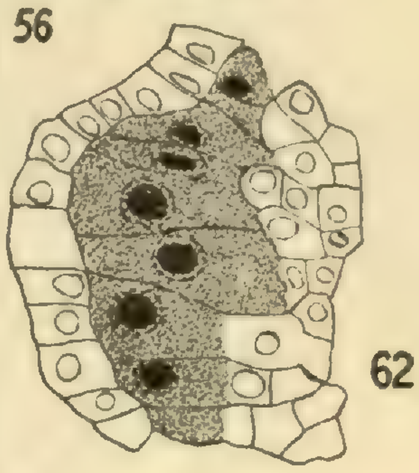

59


n.ep.
60

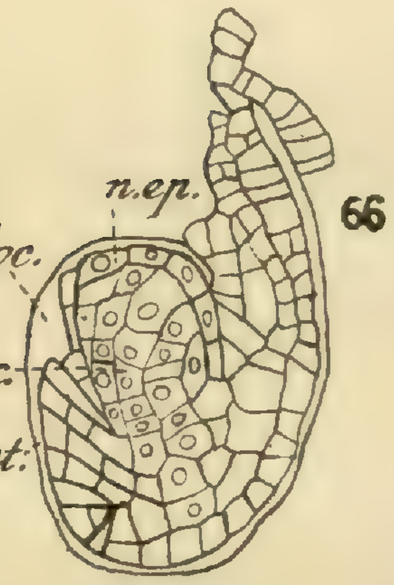
61
int.

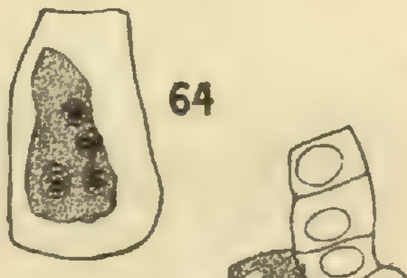

63


56
n.ep.

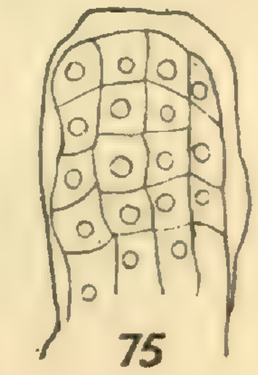

62

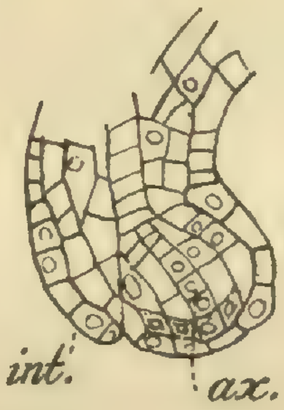
n.ep.
int.
65


n.ep.
loc.
ax.
int.
66

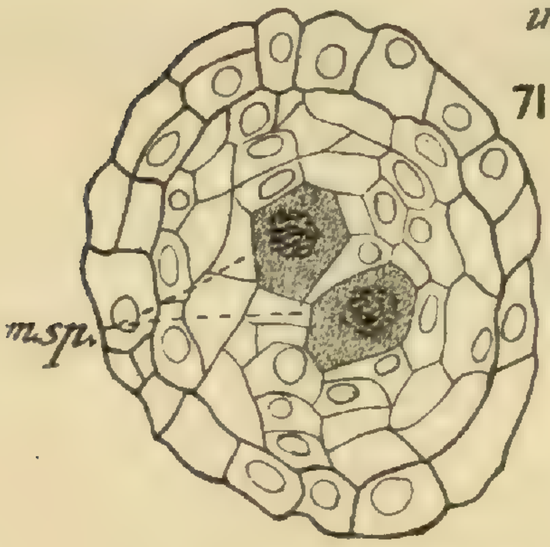

64

int.
69
par.
n.ep.
68
int.

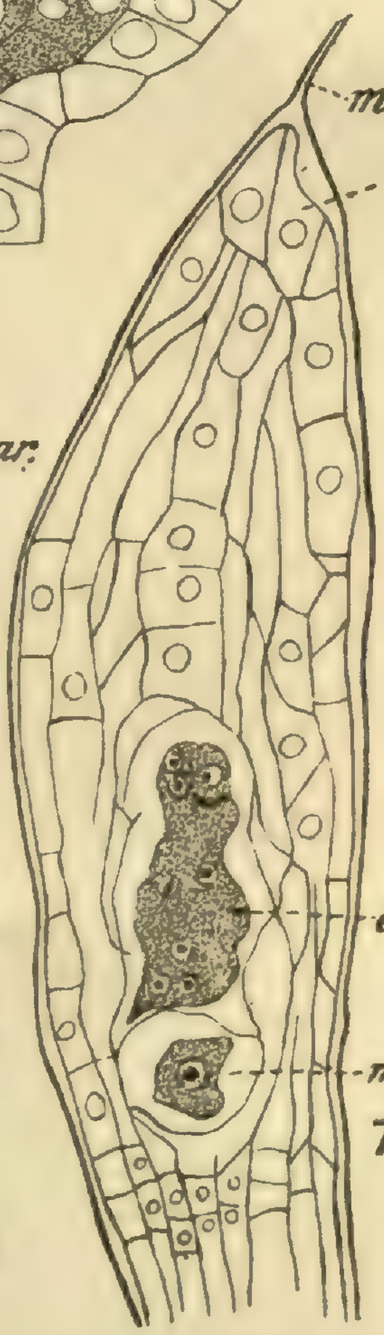

75


int.
ax.
67

int.
m.
n.ep.
ax.
76

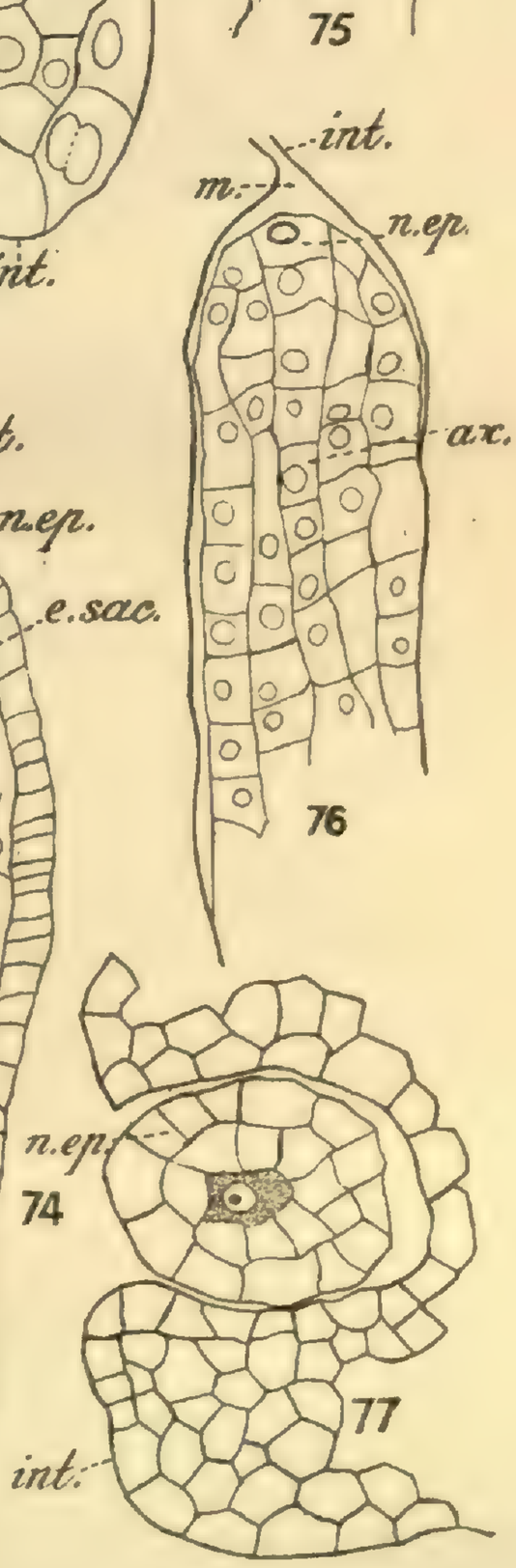

71
m.sp.

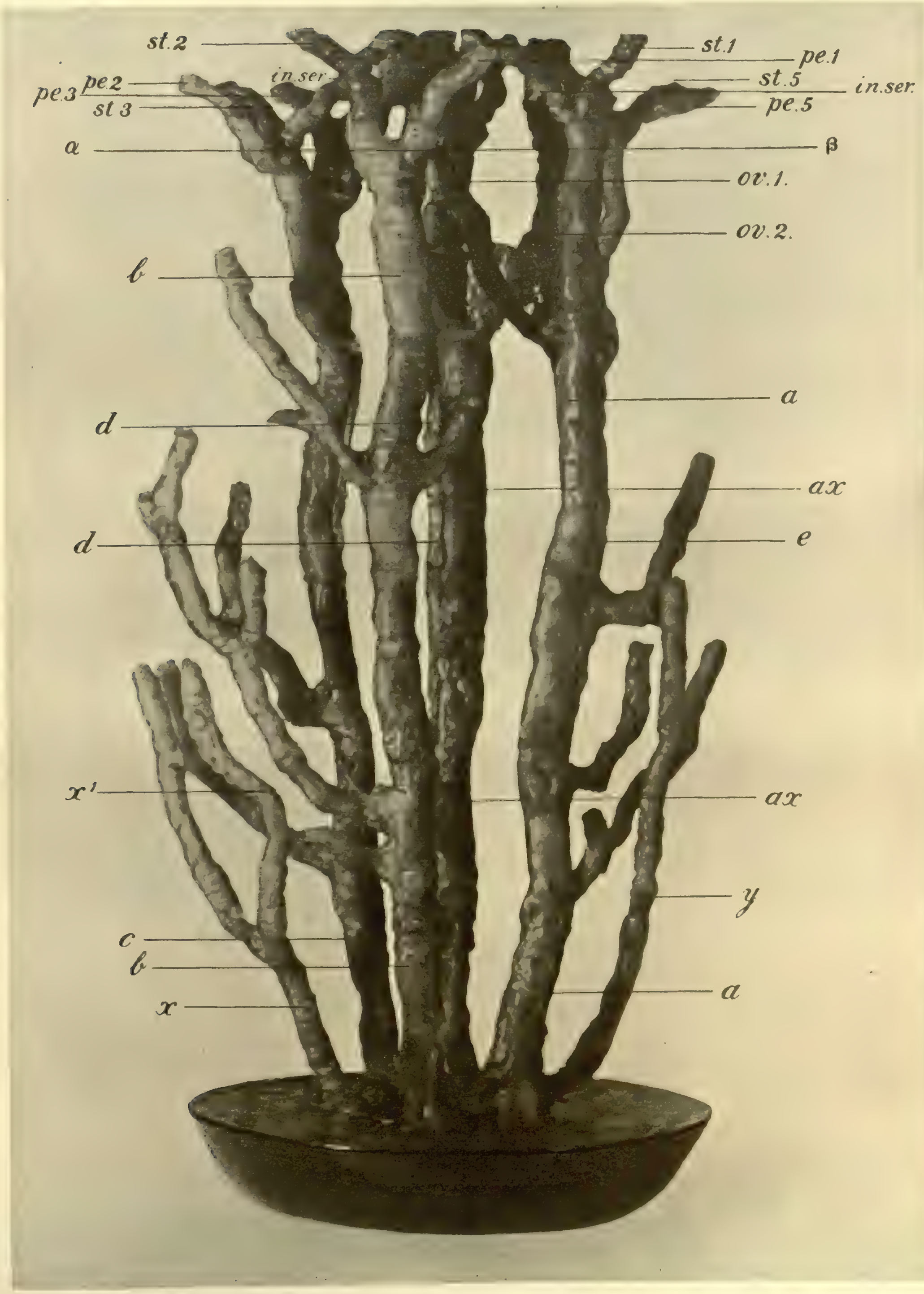
n.ep.
int.
par.
m.sp.
70
e.sac.


m.
n.ep.
e.sac.
m.sp.
72

m.
int.
n.ep.
e.sac.

arch.
n.ep.
73
int.


n.ep.
74
77
int.



A.S.H. phot. Grout, sc. & imp

VASCULAR SYSTEM OF THE FLOWER OF *VIBURNUM LANTANA*

LINNEAN SOCIETY OF LONDON.

MEMORANDA CONCERNING TRANSACTIONS.

The First Series of the Transactions, containing both Botanical and Zoological contributions, has been completed in 30 Vols., and a few entire sets are still for sale. Only certain single volumes, or parts to complete sets, may be obtained at the original prices. The price of the Index to Vols. 1–25 is 5*s.* to the public, and 6*s.* to Fellows; to Vols. 25–30, 4*s.* to the public, and 3*s.* to Fellows.

The Second Series of the Transactions is divided into Zoological and Botanical sections. The prices of the Botanical parts of these which have been published are as undermentioned. (For the Zoological parts see Zoological wrapper.)

SECOND SERIES.—BOTANY.

Volume.	When Published.	Price to the Public. £ s. d.	Price to Fellows. £ s. d.
I.	Parts I.–IX. (complete). 1875–80.	8 1 0	6 1 0
II.	Parts I.–XVI. (complete). 1881–88.	6 16 10	5 2 3
III.	Parts I.–XI. (complete). 1888–94.	7 12 10	5 14 8
IV.	Parts I. IV. (complete). 1894–96.	3 13 4	4 5 0
V.	Part I. 1895.	0 9 0	0 6 9
	Part II. 1895.	0 12 0	0 9 0
	Part III. 1896.	0 8 0	0 4 6
	Part IV. 1896.	1 0 0	0 15 0
	Part V. 1896.	0 14 0	0 10 6
	Part VI. 1896.	0 4 0	0 3 0
	Part VII. 1897.	0 4 0	0 3 0
	Part VIII. 1897.	0 6 0	0 4 6
	Part IX. 1899.	0 12 0	0 9 0
	Part X. 1899.	0 6 0	0 4 6
	Part XI. 1899.	0 7 0	0 5 3
	Part XII. 1899.	0 12 0	0 9 0
	Part XIII. 1900.	0 1 6	0 1 2
	Part XIV. 1900.	0 3 0	0 2 3
	Part XV. 1901.	0 8 0	0 6 0
VI.	Part I. 1901.	1 10 0	1 2 6
	Part II. 1901.	0 8 0	0 6 0
	Part III. 1902.	0 18 0	0 13 6
	Part IV. 1903.	0 8 0	0 6 0
	Part V. 1903.	0 8 0	0 6 0
	Part VI. 1903.	0 12 0	0 9 0
	Part VII. 1904.	0 12 0	0 9 0
	Part VIII. 1904.	0 12 0	0 9 0
	Part IX. 1904.	0 7 0	0 5 3
	Part X. 1904.	0 14 0	0 10 6
	Part XI. 1905.	0 8 0	0 6 0

SECOND SERIES.—BOTANY (*continued*).

Volume.	When Published.	Price to the Public. £ s. d.	Price to Fellows. £ s. d.
VII.	Part I. 1904.	0 5 0	0 3 9
	Part II. 1905.	0 6 0	0 4 6
	Part III. 1906.	0 3 0	0 2 3
	Part IV. 1906.	0 7 0	0 5 3
	Part V. 1907.	0 10 0	0 7 6
	Part VI. 1907.	0 4 0	0 3 0
	Part VII. 1907.	0 6 0	0 4 6
	Part VIII. 1908.	0 5 0	0 3 9
	Part IX. 1908.	0 2 6	0 2 3
	Part X. 1908.	0 7 0	0 5 3
	Part XI. 1909.	0 4 0	0 3 0
	Part XII. 1909.	0 12 0	0 9 0
	Part XIII. 1909.	0 5 0	0 3 9
	Part XIV. 1909.	0 6 0	0 4 6
	Part XV. 1910.	0 6 0	0 4 6
	Part XVI. 1912.	0 3 0	0 2 3
	Part XVII. 1912.	0 8 0	0 6 0
	Part XVIII. 1912.	0 5 0	0 3 9
	Part XIX. 1912.	0 3 0	0 2 3
	Part XX. Index.	0 3 0	0 2 3
VIII.	Part I. 1913.	1 0 0	0 15 0
	Part II. 1913.	0 8 0	0 6 0
	Part III. 1913.	0 8 0	0 6 0
	Part IV. 1913.	0 4 0	0 3 0
	Part V. 1913.	0 10 0	0 7 6
	Part VI. 1914.	0 12 0	0 9 0
	Part VII. 1914.	0 12 0	0 9 0

2nd Ser. BOTANY.] [VOL. VIII. PART 3

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

NOTES ON THE MORPHOLOGY OF CERTAIN STRUCTURES CONCERNED IN REPRODUCTION IN THE GENUS GNETUM.

By H. H. W. PEARSON, Sc.D., F.L.S.,

HENRY BOLUS PROFESSOR OF BOTANY IN THE SOUTH AFRICAN COLLEGE.

AND

ON ISOETES JAPONICA, A. Br.

By CYRIL WEST, F.L.S., and H. TAKEDA, D.I.C.

LONDON:

PRINTED FOR THE LINNEAN SOCIETY

BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON-HOUSE, PICCADILLY, W.;

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

December 1915.

IX. *Notes on the Morphology of certain Structures concerned in Reproduction in the Genus* Gnetum *. *By* H. H. W. Pearson, *Sc.D., F.L.S., Henry Bolus Professor of Botany in the South African College.*

(Plates 31, 32.)

Read 4th June, 1914.

The following is an account of an investigation of material already described †, together with further supplies ‡, for which I am indebted to

1. Mr. J. Gossweiler (*Gnetum africanum*).
   - A. Collected at Montobello, Angola, in February 1912.
   - B. From the same locality, collected in December 1912.
2. Dr. R. H. Lock (*Gnetum Gnemon*).
   - C. Collected in Ceylon.
   - D. Collected in Ceylon on various dates between August 5 and October 27, 1912.
3. Mr. I. H. Burkill.
   - E. Collected in Singapore, August 1913.

In all these cases the ovules and male spikes were carefully fixed in various fixatives—weak Flemming's solution, alcohol formalin, mercuric chloride solution, and chromo-acetic acid. While the fixation was usually successful, delicate structures have frequently suffered to some extent in transmission. Consequently the free-nuclear stages of the embryo-sac are somewhat contracted, and no trustworthy information regarding the structures in the pollen-tube and fertilization has yet been obtained. Stages in the development of the pro-embryo and embryo have been figured, but their publication is postponed until the account can be made more complete.

A. The Spike and the Female Flower. (*G. Gnemon.*)

Most writers have hitherto referred to only two forms of spike in *Gnetum*, viz. :—

1. The pure female spike bearing ovules, each with three envelopes. Many of these are normally arrested; the rest are fertile.
2. The pseudo-androgynous (a male) spike, bearing functional male flowers and infertile ovules with two envelopes only.

* Percy Sladen Memorial Expeditions in South-West Africa (assisted by grants from the Royal Society), Report No. 22.

† Pearson, 1912.

‡ Material of *G. scandens*, recently sent from Darjeeling by Mr. G. H. Cave, awaits investigation.

A third form has recently been described *, viz. :—

3. A pure male, usually without any trace of infertile ovules or their envelopes. This has so far been described only in the two African species, *G. africanum* and *G. Bucholzianum*. In *G. africanum* an incomplete female flower is very rarely present.

For many years there has been reason to suspect that still another form of spike sometimes occurred in certain species, particularly in *G. Gnemon*. Lotsy † refers to "a plate in Rumphius picturing a branch of a male tree of *Gnetum Gnemon* with some apparently normal adult fruits." Strasburger ‡ found in an androgynous inflorescence of *G. Brunonianum* (=*G. Gnemon*) received from Beccari that " waren die männlichen Blüthen bereits abgeblüht, theilweise abgefallen, die weiblichen noch erhalten." Commenting upon this and upon statements made by Blume § and Griffith ‖ that the 2-enveloped ovules of the male spike may later develop a middle envelope, Strasburger remarks ¶ :—" Könnte vermuthet werden, dass diese Blüthen (*i. e.* incomplete female flowers of the 'male' spike) bei *Gnetum Brunonianum* sich auch noch weiter entwickeln, ja dass es auch noch andere *Gnetum*-Arten giebt, bei welchen die weiblichen Blüthen der androgynen Blüthenstände noch keimfähige Samen erzeugen; unmöglich ist dieses nicht, mir persönlich aber kaum wahrscheinlich."

On a later page Strasburger ¶ writes:—" Die einzige positive Angabe über drei Hüllen an der weiblichen Blüthe der pseudo-androgynen Blüthenstände, wo sicher nur solche vorlagen, wird von Tulasne ** für *Gnetum Leyboldi* gemacht, allein aus den eigenen Figuren Tulasne's †† ist zu ersehen, dass diese Angabe nur auf einer Täuschung beruht." Lotsy ‡‡ obtained from a collector in the neighbourhood of Buitenzorg " a male branch with a young fruit very much larger than the female flowers in the androgynous infloresences." This inflorescence was broken, and bore no male flowers, but it came from a male tree. The " fruit " which it bore possessed three normal integuments, but was not fertilized. " Consequently, we have found here on a *male* tree a female flower corresponding to those which occur normally on the female trees, it possessing like these three integuments and not two like the female flowers of the androgynous inflorescences."

In the material of *Gnetum Gnemon* now under consideration, ovules with three, occasionally with *four* (see figs. 2, 3) envelopes occur, the former not uncommonly, in the spikes which bear the male flowers. These complete female flowers when present are usually found in the lowest node. They are larger than the incomplete flowers, and in the cases observed it was not certain that they originated in the uppermost ring of the node; the male flowers of the nodes which bear them appear always to be fewer in number than at ordinary nodes. In connection with the occurrence of these complete flowers in the lower nodes of the spike, the following observation made by Mr. I. H. Burkill may be of interest. He writes from Singapore (20. viii. 13) :—" After flowering,

* Pearson, 1912.
§ Blume, 1848.
** Tulasne, 1858, p. 116.
† Lotsy, 1899, p. 53.
‖ Griffith, 1859, p. 301.
†† Tulasne in Mart. Fl. Bras. iv. 1. Tab. 103.
‡ Strasburger, 1872, p. 105 *et seq.*
¶ Strasburger, *l. c.* p. 110.
‡‡ Lotsy, *l. c.*

the upper part of the spike (*i. e.* androgynous of *G. Gnemon*) breaks off and falls to the ground, leaving the flowers of the lowest axils." In the first case found there were two such flowers at the lowest node; one had three envelopes, the other four (figs. 2, 3); each contained more than one embryo-sac, all in an early free-nucleate condition. The former contained many pollen-grains in the micropyle; two of these are shown in detail in fig. 9. This node bore no incomplete female flowers; these were, however, present in their usual position at the upper nodes.

This observation is of interest, in that it undoubtedly explains the statements of previous authors referred to above. Since these ovules do become pollinated, it may be presumed that fertilization ensues in some cases at least and that fertile seeds may be borne upon the spikes which produced the male flowers. In other words, in *Gnetum Gnemon*, as probably also in *G. Leyboldi* and other species, there is found a truly androgynous as well as a pseudo-androgynous spike.

The four types of spike now described establish a sequence ranging from the strictly unisexual to the bisexual, or conversely, which leaves no doubt that the two commoner types are members of the same evolutionary series. Whether this series progressed in two directions from a primitive bisexual form or from two unisexual inflorescences towards a combined type, has been a fruitful subject for discussion. Wettstein * holds the latter view for all the genera of the Gnetales. The principal points in his argument are the following:—

1. The primitive flower of the Gymnosperm was unisexual. Bisexual inflorescences are unknown in the Cycads, but are relatively common in the higher forms.
2. *Ephedra campylopoda* (the only member of the genus in which a bisexual inflorescence occurs at all commonly) does not, in its general characters, give the impression of being a primitive form.
3. The archegonia of the female flower of the androgynous spike of *G. campylopoda* show no signs of reduction, although they apparently do not become fertilized.
4. If the occurrence of ♀ flowers in this androgynous inflorescence is really due to reversion, then a similar reversion would be expected to occur in the ♀ inflorescence.
5. If, on the other hand, the appearance of bisexuality is due to "progressive mutation" (as Wettstein believes), then it would be expected to appear in the ♂ inflorescence rather than in the ♀, on account of the normally unlimited growth of the former.

Wettstein quotes the evidence of Blume, Griffith, and Lotsy as to the occasional appearance of a bisexual inflorescence in *Gnetum*, and is inclined to think that "auch morphologisch diese 'zweigeschlechtigen' männlichen Blüten von *Welwitschia* analog erklärt werden können, wie die zweigeschlechtigen Inflorescenzen bei *Ephedra*."

These arguments are not convincing. No. 1 would have greater force if the living Gymnosperms formed a monophyletic group. The history of certain sections of the

* Wettstein, 1907, p. 28.

group is obscure, and it is highly improbable that its complete elucidation will establish the view that they represent a simple series. The statement contained in No. 2 is no doubt true, but has it necessarily any bearing upon the point at issue? The conditions which influence the development of the vegetative organs do not necessarily affect the reproductive parts. An angiospermic parasite, for example, frequently shows extreme reduction in all parts of the plant-body save in those concerned with reproduction, which may, indeed, be of a highly specialized character. The fact that the archegonia of the imperfect female flowers of *Ephedra campylopoda* show no signs of reduction is not conclusive, if true. An argument based upon *Ephedra* must almost certainly apply to *Gnetum* and *Welwitschia*. In the latter, sporogenous tissue is not organized in the so-called hermaphrodite flower; in the former, gametes do not appear in the incomplete female flower. The female flower of *Ephedra campylopoda* is less incomplete than that of either of the other two genera, but if reduction can account for the one it must explain all. The last two points are of less importance. If an Angiospermic species with polygamous flowers may be held to be descended from a more primitive form with hermaphrodite flowers, a similar explanation of the occurrence of female, male, and more or less hermaphrodite inflorescences or spikes in the Gnetales is not ruled out. Since the date of Wettstein's paper it has been shown that *E. campylopoda* is entomophilous *; the same is true for *Welwitschia* †, and not improbable for *Gnetum* ‡. In all cases it is probable that the ovule of the "hermaphrodite" spike or flower has become specialized in connection with insect-pollination. This specialization is much more likely to have occurred through the reduction in some or all of the parts of a primitively functional hermaphrodite flower than by "progressive mutation." In the latter case the fact that a new and previously functionless structure adapted to attract insects bears so curious a resemblance to a functional female flower would be difficult to explain.

Strasburger § discussed the question fully and, at least for *Welwitschia* and *Ephedra*, arrived at the conclusion that the female flower in each case represented an advanced stage in the reduction of a primitive hermaphrodite flower, and that the pseudo-hermaphrodite flower of *Welwitschia* represents an intermediate stage passed in the course of this reduction. While it is not impossible that the actual course of events has been more complicated than is here suggested, Strasburger's view that the existing structures are the result of a process of reduction seems to be in closer accord with the facts than the contrary opinion of Wettstein ‖.

Both the female and the pseudo-androgynous spikes of *Gnetum Gnemon* in the specimens under notice very frequently bear a single terminal ovule; this was also recorded by Strasburger ¶. This fact, together with the occasional reduction of the male spikes to two nodes separated by an internode (*G. Bucholzianum* **) and the presence of "a ring of complex groups of vascular strands arising from the branches in

* Porsch, O., 1910.
† Pearson, 1909.
‡ Karsten, 1893; Lotsy, 1899, &c.
§ Strasburger, 1872, p. 150 *et seq.*; see also Goebel, 1905.
‖ Lignier et Tison, 1912, p. 178.
¶ Strasburger, 1872, p. 158.
** Pearson, 1912.

the base of the female flower of *Gnetum Gnemon*" *, afford some support to the view that the primitive inflorescence from which the present complex spikes have arisen was of the nature of an axis bearing a terminal ovule surrounded by a single ring of male flowers * (or perhaps anthers).

In the ovule with four integuments, referred to above (fig. 2), there is no trace of the "ring of complex groups of vascular strands" described by Miss Berridge for the normal ovule with three envelopes, but the three lower of the envelopes possess an apparently equivalent vascular supply. This might, perhaps, be regarded as indicating that this reduced ring of vascular tissue is a vestige, not of a ring of male elements, as Miss Berridge suggests †, but of a missing fourth envelope. On the other hand, it will be seen on reference to the figure that the second and third envelopes appear to arise from a common base—indicating, perhaps, a doubling of the original middle integument. This suggestion is of interest when compared with the accounts given of the development of the incomplete female flowers. Lotsy ‡ finds that a middle envelope is present in a rudimentary condition in the younger stages, but later is unrecognizable. It therefore seems probable that the middle envelope is less stable in character than either of the other two; that it is liable to be suppressed or duplicated according to circumstances. It is at least improbable that the outermost envelope is supernumerary. Before it was cut, the ovule enclosed in its envelopes had a perfectly normal appearance, and there was nothing to suggest that its outer covering was in any way different from that of an ordinary complete female flower, and as far as the outer envelope itself is concerned, this resemblance is seen also in the sections. In any case, it is clear that in the present state of our knowledge some degree of caution should be exercised in assigning any of the three normal envelopes to a particular morphological category.

The same ovule shows another feature of interest which appears not to have been previously described. A tangential section (fig. 3) shows a bud arising between the outer and the succeeding envelopes (*b*). As this is the only instance of the kind observed, it is not certain that the bud stands opposite the median line of one of the primaries from which the outer envelope is derived. Also its vascular supply cannot be determined at this stage. It may, however, be presumed that it is truly axillary. If so, the foliar character of this envelope is beyond doubt. If the view suggested above, that the middle integument in this ovule is duplicated, is correct, and the outermost of the four envelopes is therefore homologous with the outermost of the three of a normal flower, an interesting conclusion is suggested by the presence of this axillary bud. For it shows that there exists a tendency to the development of axillary structures by which the spike of *Gnetum* might arise by "proliferation" from a primitive inflorescence (or flower) bearing a single terminal ovule. A similar origin for the male spike of *Welwitschia* has already been suggested by Wieland §. Also, if this is the true outer envelope, the presence of a bud in its axil is in favour of the conclusion that the origin of the flower-envelope of the Gnetales is to be sought, not in the sterilization

* Pearson, 1912.

† Berridge, 1912.

‡ Lotsy, 1899.

§ Wieland, 1908.

of sporophylls, but in the specialization of barren leaf-structures *; and it might also be regarded as in opposition to the current view that the outer envelope is a perianth †. On the other hand, if a perianth homologous with that of the Angiosperms is present in the Gnetales, it is not probable that in this group it will have attained the high degree of specialization which is characteristic of the perianth of the former. But the unqualified use of the term "perianth" implies a homology which may be correct, but of which there is at present no direct proof.

The nature of the axillary bud is uncertain (fig. 3); but an examination of the whole series of sections passing through it gives the impression that it is a female flower, complete or incomplete, in an early stage of development.

The material at present available does not contain early stages of development of complete female flowers. Very young incomplete female flowers are shown in Pl. 31. figs. 4 and 5. Slight swellings on the axis (figs. 4 and 5, *m*), between the insertions of the outer and inner envelopes, are doubtless identical with those considered by Lotsy ‡ to represent a rudimentary middle envelope. If so, these figures may be regarded as confirming the statement that these envelopes arise in acropetal succession, which has been made by previous writers (Beccari, Strasburger, Karsten, and Lotsy §). They therefore correspond in development to the envelopes of the complete female flower as described by the same authors. The same order of succession in development is found in the ovular envelopes of *Ephedra* ‖ and *Welwitschia* ¶. While all recent investigators are in agreement on this point, Coulter and Chamberlain ** state, without discussion, that in all three genera "there are two integuments which arise in basipetal succession."

B. The Male Flower Microspore and Pollen-Grain. (*G. Gnemon.*)

A single young pseudoandrogynous spike of *G. Gnemon* has been available for study. It has yielded certain stages in the development of the male flower which have not been previously described for this species. Karsten †† figures three stages ranging from the early condition of the envelope to the periclinal division of the primary tapetal layer. Lotsy's observations on the germination of the microspore have not yet been published ‡‡.

The internodes of the spike are somewhat longer than those of *G. scandens* §§, but much shorter than in the African species ‖‖. As in *G. scandens*, the flowers at the nodes of *G. Gnemon* receive their vascular supply from a single series of strands arising from the leaf-traces ¶¶, and the capsule is without the large mucilage cavity which is so marked a feature in the African species ***.

The male flower of *G. Gnemon* usually bears two anthers. These are always placed transversely to the axis of the spike, so that a longitudinal median section of the latter either passes between them or through one of them. Occasionally four anthers are

* Goebel, 1905.
† Lotsy, 1899, pp. 63, 64.
‡ Lotsy, 1899, pl. 3. fig. 14.
§ Beccari, 1897; Strasburger, 1879; Karsten, 1893; Lotsy, 1899.
‖ Jaccard, 1894.
¶ Hooker, 1863; Pearson, 1906.
** Coulter and Chamberlain, 1910.
†† Karsten, 1893, figs. 12–14.
‡‡ Lotsy, 1899, p. 82.
§§ Pearson, 1912, fig. 1 *a*.
‖‖ Pearson, 1912, figs. 1 *b* & *c*.
¶¶ Pearson, 1912, fig. 2; Thoday, 1912.
*** Pearson, *l. c.* figs. 2, 3, & 4.

present (Pl. 31. fig. 6). When this is the case the two supernumerary anthers decussate with the others. The vascular structure of the axis bearing more than two anthers has not been investigated.

The single envelope at the stage shown in fig. 7 has the form of an approximately equal collar arising from the base of the axis. Later on, growth is confined to two points at right angles to the plane in which the anthers lie, the posterior lobe so produced overlapping the lower or anterior *. The origin of the sporogenous tissue and tapetal layers is as described both for this species † and for *G. africanum* ‡. The elongation of the floral axis commences at about the same time as the periclinal divisions arise in the primary tapetum layer. Up to this time the anther primordia are sessile in the minute axis, which bears the perianth-collar (fig. 7). The axis thus formed by intercalary growth finally attains such a length that it may project as much as 3 mm. beyond the edge of the subtending bract-capsule. Its elongation is probably not completed when the dehiscence of the anthers commences.

There has been some discussion as to the morphological character of this apparent axis supporting the anthers. Strasburger regarded it and its homologue in the male flower of *Ephedra* as being of the nature of a true axis §. More recently, however, evidence has been adduced in support of the view that the antherophore is not an axis but a foliar structure formed by the fusion of what must be regarded as the filaments of the anthers ‖. This opinion is to some extent supported for *Gnetum* by the late origin of this structure by intercalary growth. As pointed out by the authors cited, this view has the advantage of offering a rational basis for the comparison of the male flower of *Welwitschia* with those of *Ephedra* and *Gnetum*. If the vascular knots which Miss Berridge ¶ describes as existing between the origins of the outer and middle envelopes of the female flower are the vestiges of a whorl of microsporophylls, the male flower of *Gnetum* may well be derived from a hermaphrodite structure not essentially different from that which persists in a reduced form in *Welwitschia*.

The development of the sporogenous tissue has not been traced in detail in this species. Several stages, however, have been seen which correspond exactly with those described for *G. africanum* **. As in the latter species, the microspore mother-cell is chambered (fig. 8), the limiting wall and the septa being in both cases very thick and mucilaginous ††. Coulter determined the reduced number of chromosomes in the homotypic division of the mother-cell of this species to be 12 ‡‡.

The germination of the pollen-grain has not been followed in detail; its results are apparently the same as in *G. africanum* §§. The exine of the adult pollen-grain is thick, covered externally by minute protuberances and without any obvious pores on their areas ‖‖. The two pollen-grains shown in fig. 9 were found, with others, in the micropylar tube of the ovule of fig. 2. The nuclei were easily visible in most of these

* Pearson, 1912, pl. 60. fig. 2.
§ Strasburger, 1872, p. 157.
** Pearson, 1912.
§§ Pearson, 1912, fig. 20.
† Karsten, 1894, t. 8. fig. 14.
‖ Thoday and Berridge, 1912.
†† *Cf.* Pearson, 1912, fig. 15.
‖‖ *Cf.* Karsten, 1893, p. 358; Strasburger, 1872, p. 156.
‡ Pearson, 1912, figs. 5, 6.
¶ Berridge, 1912.
‡‡ Coulter, 1908.

grains; some contained two, others three. All appeared to be quite free, and there was no clear indication of the presence of a generative "cell" such as Karsten records for later stages of various species and Lotsy * for *G. moluccanum*. The adult pollen-grains of various Indo-Malayan species † and of *G. africanum* ‡ possess three nuclei. In all cases described, one of these (presumably prothallial in character) disappears before the pollen-grain reaches the micropyle. In *G. Gnemon* it would appear that all three may persist until pollination has occurred, or one of the three may disappear as in other species. Whether the third always disappears before the pollen-grain germinates is not known.

C. The Macrospore and Endosperm. (*G. africanum*.)

The structure of the ovule of *G. africanum* has been described in detail by Mrs. Thoday §, that of *G. Gnemon* and of other species by various authors ‖. Much has also been written upon the embryo-sac, embryo, and endosperm, especially of *G. Gnemon* ¶; there are, nevertheless, still very important gaps in our knowledge of these structures. The origin and morphology of the endosperm is a subject regarding which further information is very desirable. Two types of endosperm are known to occur in the Gnetales. One of these, a prothallus bearing archegonia, is characteristic of *Ephedra*. The second, arising from cells uniformly constituted by the fusion of numerous nuclei, occurs in *Welwitschia*. When the latter was first described **, it was suggested that the morphological differences between these two types of endosperm were of a more or less fundamental character; that *Ephedra* retains the intrasporic prothallus of the lower spermaphytes; that the endosperm of *Welwitschia* is morphologically distinct from anything hitherto described for the gymnosperms, representing, perhaps, an early term in an evolutionary series which has ended in the highly specialized endosperm of the Angiosperms—a structure whose morphological value is doubtful. However they are to be explained, the facts themselves are important. Apart, then, from any morphological interpretation which may be placed upon it, it is clearly a matter of some interest to determine whether in respect to its endosperm *Gnetum* is to be classed with *Ephedra* or with *Welwitschia*.

Since previous investigators have left no room for doubt that the female gametes of *Gnetum* are free nuclei as in *Welwitschia*, and that in both cases the accessory structures of the archegonium are absent ††, it would appear probable, *a priori*, that the endosperm of *Gnetum* also resembled that of *Welwitschia*. Although the details of endosperm formation were not followed either by Karsten or by Lotsy, their accounts, read in the light of what is now known for *Welwitschia*, contain a little internal evidence in favour of a homology with the latter ‡‡.

* Lotsy, 1899, p. 94.
† Karsten, 1893, p. 359; Lotsy, 1899, p. 94.
‡ Pearson, 1912.
§ Thoday, 1911.
‖ Strasburger, 1872, 1879; Karsten, 1892, 1893; Lotsy, 1899; Berridge, 1911, 1912; &c.
¶ Bower, 1882; Karsten, *l. c.*; Lotsy, *l. c.*; Coulter, 1908.
** Pearson, 1909.
†† G. Lignier et Tison, 1912, p. 171.
‡‡ Pearson, 1909, pp. 356–358.

Karsten records that in the species investigated by him *, fertilization occurs while the sac is still unseptate and all the nuclei are free. After fertilization the lower part of the sac (in *G. Rumphianum* and *G. ovalifolium*) becomes cellular by septation, the "cell" frequently containing two or more nuclei. A similar condition is found also in *G. edule* †. At length, apparently, all the cells of the endosperm become uninucleate ‡.

Lotsy found § that in *G. Gnemon* the lower (sterile) part of the sac becomes septate *before* fertilization, and that at first some at least of the compartments into which it is divided are multinucleate. All eventually become multinucleate ‖.

In *G. Ula* ¶ fertilization has not been described, and Lotsy was at first of opinion that this species is parthenogenetic. More recently, however, he is inclined to interpret differently the structures originally supposed to be apogametic embryos, and to regard them as the homologues of the embryo-sac tubes of *Welwitschia* **. However this may be, in this, as in the other species described formerly by Lotsy and by Karsten, the lower part of the sac becomes septate to form a solid endosperm tissue.

In 1908, Coulter †† reinvestigated the embryo-sac of *Gnetum Gnemon*. He encountered the difficulty which has so far confronted every one who has attempted to study *Gnetum*, viz. the absence of "many intervening stages" from his material. Coulter's conclusions differ in some important respects from those of Lotsy. He describes a clearly differentiated region of nucellar tissue at the base of the sac under the name of "pavement tissue." At the time of the appearance of this tissue the embryo-sac contains free nuclei throughout its length, and Coulter concludes that Lotsy's "antipodal tissue is clearly this glandular pavement tissue developed in the chalaza": in other words, Lotsy's primary endosperm is a part of the nucellus which, as Coulter correctly states, is later destroyed by the advance of the true endosperm ‡‡.

Lotsy reaffirms his previous statements §§ without, however, being able to throw any new light upon the origin of the endosperm.

In the related genus *Welwitschia* ‖‖ the whole sac becomes septate, before pollination, into multinucleate compartments. In those compartments which contain many nuclei, nuclear fusion occurs. The uninucleate cells so formed are primary endosperm cells, all of which arise in this way. These occupy almost the whole (frequently the whole) of the chalazal two-thirds or three-quarters of the sac. In those compartments which enclose fewer nuclei, the latter remain free and form the functional gametes; the walls of the compartments grow out into the nucellar cap forming the embryo-sac tubes.

The youngest ovules of *G. africanum* available are just at the stage at which the upper half of the ovule emerges beyond the edge of the cupule (Pl. 31. fig. 1). In the youngest of these the embryo-sac contained four free nuclei ¶¶. As the sac elongates and the nuclei increase in number, they depart from the regular peripheral arrangement

* Karsten, 1893 (2).
† Karsten, 1892, fig. 9 A.
‡ Karsten, 1892, fig. 21.
§ Lotsy, 1899.
‖ Lotsy, 1899, p. 98.
¶ Lotsy, 1903.
** Lotsy, 1911, pp. 350–352.
†† Coulter, 1908.
‡‡ *L. c.*; Coulter and Chamberlain, 1910, p. 383.
§§ Lotsy, 1911, p. 355.
‖‖ Pearson, 1909.
¶¶ *Cf.* Lotsy, 1899, fig. 25 (after Strasburger).

which characterizes the earlier stages, and tend to become aggregated more or less in the chalazal end of the sac (fig. 9). At this stage the embryo-sac does not show the "biscuit-like" shape described and figured for a slightly later stage of *G. Gnemon* *. Nor, in fact, does it eventually assume this form. As the nuclei further increase in number, the aggregation at the chalazal end becomes more marked, and occupies approximately the lower half of the sac; the cytoplasm of this region also becomes much less vacuolated than in the micropylar half. It is clear, therefore, that the differentiation of the sac into micropylar (fertile) and chalazal (sterile) parts is recognizable at least as early in *Gnetum* as in *Welwitschia*. Meantime the nucellar tissue immediately beneath the chalazal end of the sac commences to form what Coulter has called the "pavement tissue" †, a fairly regular tissue in which the cells are more or less strictly arranged in longitudinal rows (Pl. 31. fig. 13).

The next important change in the embryo-sac is the blocking-out of the cytoplasm of the lower half into compartments. At the time of its occurrence the sac seems to be in a particularly delicate state, and more liable to contraction than at any other period of its history—a characteristic of the *Welwitschia* sac at a corresponding stage in its development ‡. The first stage of septation—such as that figured for *Welwitschia* §—has not been seen. The youngest stage found (fig. 12), probably slightly contracted, shows that each compartment possesses a definite limiting membrane which, however, does not yet react to cellulose stains ‖. So far, then, the septation of the lower end of the sac presents many similarities with that of *Welwitschia*. The outlines of each compartment are irregular, and the sectional area varies within wide limits. Many sacs in this condition have been examined. Every compartment contains more than one nucleus; most can be seen to possess five or more. The upper part of the micropylar end of the sac of fig. 12 is shown in fig. 11. The cytoplasm is irregularly vacuolated and shows no sign of septation; the nuclei are fairly uniform in size and appearance, both among themselves and with the free nuclei enclosed in the lower compartments. Their distribution in the cytoplasm is irregular. Area for area, the number of nuclei in the upper unseptate part of the sac is smaller than in the lower half. According to Lotsy ¶, this micropylar end of the sac remains unseptate and the nuclei unchanged until fertilization occurs.

In the septate chalazal region of the sac the nuclei in each compartment become massed together, and the constituents of each mass fuse to form a single nucleus. The process of fusion, as in *Welwitschia*, appears to be of a simple character. The contiguous portions of the nuclear membranes cease to be visible (Pl. 32. fig. 15), and gradually the outline of the whole mass assumes a more regular form, in which the individuality of the fusing nuclei is lost. For a time each fusion-nucleus contains several nucleoli (fig. 16), which, however, are soon reduced to a single one, doubtless by fusion ** (figs. 19, 22). The fusions are by no means simultaneous, for in a single sac will

* Lotsy, 1899, p. 92, fig. 28. † Coulter, 1908. ‡ Pearson, 1909, p. 347.
§ Pearson, 1912, figs. 22, 23. ‖ *Cf.* Pearson, *l. c.* fig. 32. ¶ Lotsy, 1899, p. 93.
** *Cf.* Pearson, *l. c.* figs. 36, 38 A; Tischler, 1900, figs. 23–36.

be found compartments still containing free nuclei side by side with those which by the completion of the nuclear fusion have become uninucleate cells (Pl. 32. figs. 19, 22). Fig. 22 shows the completion of what may be described as the primary endosperm. Pollination usually occurs between the stages of figs. 18-22, while the nuclei of the micropylar end of the sac appear to be in exactly the same condition as they were when the chalazal end became septate preparatory to nuclear fusion in that region (*cf.* Pl. 31. figs. 11, 14; Pl. 32. figs. 16, 20, 21).

It appears then, that while the nucellar "pavement tissue" described by Coulter in *G. Gnemon* is present in *G. africanum*, this species also shows the fertilization antipodal tissue of the embryo-sac, such as was found by Lotsy in *G. Gnemon*, the existence of which has been denied by Coulter*. This "antipodal tissue" in the embryo-sac is the primary endosperm, consisting of cells whose nuclei are formed by fusion. The material used in this investigation has not permitted the development of the endosperm of *G. Gnemon* to be followed throughout. It does, however, show stages which leave little doubt that in this respect *G. Gnemon* and *G. africanum* are exactly alike, and that Lotsy's account in respect of the endosperm is perfectly accurate.

Lotsy has followed the growth of the pollen-tubes down to the embryo-sac in *G. Gnemon*, and although his account of fertilization is far from complete, there can be little doubt that any of the free nuclei of the upper unseptate part of the sac are capable of being fertilized—in other words, are gametes.

For the present it may be safely assumed that the same is true for *G. africanum*. If so, we are in a position to establish a comparison between the unfertilized embryo-sacs of *Gnetum* and *Welwitschia*. In the latter case we have a sac which, before septation and nuclear fusion, contains many nuclei apparently equal in origin and potentially equivalent in function. So far as is known, those of the upper or micropylar region of the sac are all of them capable of uniting with sperm nuclei to produce pro-embryos. Since in the lower part of the sac some may escape fusion, and in this case travel up into the nucellus in embryo-sac tubes†, it appears that all the nuclei of this region are of the same quality, and lose their sexuality only when they fuse together to form the single nuclei of the primary endosperm cells. So far as can be seen, *Gnetum africanum* agrees entirely with *Welwitschia*, save only that in *Gnetum* there is no septation in the micropylar half of the sac. In *Welwitschia* this septation is, perhaps, merely of the nature of an adaptation to the peculiar form of siphonogamy which prevails in this genus. It appears, then, that in *Gnetum*, as in *Welwitschia*, the sac before septation contains free, potentially fertile nuclei; that after the septation of the lower end of the sac the nuclei here lose their sexuality by fusion, while those of the upper end, which remain unfused, retain it. Therefore the primary endosperm of *Gnetum* is in all respects homologous with the primary endosperm of *Welwitschia*.

The cells of the primary endosperm of *Gnetum* soon undergo cell-division, some of them immediately after the completion of the fusion, with the result that the endosperm

* Coulter, 1908; Lotsy, 1899.

† Pearson, 1909, text-fig. p. 365; see also p. 373.

becomes a tissue composed of very unequal cells (Pl. 32. fig. 23) as in *Welwitschia* *. Later, the micropylar portion of the sac becomes filled with an endosperm tissue resembling that of the lower end. According to Lotsy, this occurs after fertilization. The origin of the upper part of the endosperm is at present not known with any certainty. Lotsy states that "a greater or smaller number of the (unfertilized) nuclei of the fertile part of the embryo-sac surround themselves with a denser protoplasm, a membrane, and thus form cells" †, and that these cells later become obliterated by the upward growth of the primary endosperm tissue below it. There is reason to think that this account may require some amendment. In any case, all but the apex of the sac—which usually becomes disorganized in *G. africanum* after fertilization—is filled with an endosperm tissue of a uniform character, and in the upper part of this the pro-embryos are embedded ‡.

D. Summary of Results.

1. *Gnetum Gnemon.*

A. A fourth type of spike bearing male flowers and both incomplete and complete female flowers is described. The latter are pollinated. This is apparently a spike which has been obscurely noticed by previous writers.

B. The complete female flower of the androgynous spike occasionally possesses four envelopes. The fourth envelope is probably due to the duplication of the middle envelope of the normal complete flower.

C. In an ovule with four envelopes, the outermost bears an apparently axillary bud.

D. Both the female and the pseudo-androgynous spikes frequently bear a single terminal ovule.

E. As described by nearly all recent investigators, the envelopes of the incomplete female flower appear in acropetal succession. A swelling on the axis between the insertions of the two integuments, considered by Lotsy to represent the aborted middle integument, is recognized.

F. The vascular supply of the pseudo-androgynous spike resembles that already described for *G. scandens*. The capsule also resembles that of *G. scandens* in that it contains no mucilage cavity.

G. The male flower usually bears two anthers; two supernumerary anthers are occasionally present.

H. The antherophore arises by intercalary growth; like that of *Ephedra*, it is probably a foliar structure representing two fused filaments.

I. The microspore mother-cell is four-chambered.

K. The pollen-grains in the micropyle contain either two or three free nuclei.

* *Cf.* Pearson, 1909, pl. 30. fig. 88. † Lotsy, *l. c.* pp. 97, 98.

‡ Coulter, 1908, fig. 7. Mrs. Thoday (1911) states that she examined "large fertilized ovules (of *G. africanum*) containing well-developed endosperm but no embryos." This is no doubt correct. But ovules of the same gathering, and probably in the same stage of development as those to which she refers, contain numerous *pro-embryos* which are easily mistaken for endosperm cells.

2. *Gnetum africanum.*

A. The youngest embryo-sac found contained four free nuclei.

B. In a later stage the free nuclei become somewhat crowded in the chalazal end of the sac.

C. About this time the "pavement tissue" appears in the nucellus below the embryo-sac.

D. When the last nuclear division in the free-nucleate sac is completed, the lower end of the sac becomes septate by the formation of division-walls of irregular form; each compartment so enclosed is multinucleate.

E. Meanwhile the micropylar half of the sac remains unseptate and its nuclei free and unchanged in appearance. So far as is known, the nuclei throughout the sac at this stage are of the same generation; they are alike in all visible characters.

F. All the nuclei in the multinucleate compartments enter into fusion; the fusion is of precisely the same character as that described for *Welwitschia*. Each multinucleate compartment thus becomes a uninucleate cell—a cell of the primary endosperm.

G. The fusion is not simultaneous in all the compartments.

H. The primary endosperm so constituted undergoes cell-division and growth. As in *Welwitschia*, the cells of the later stages of the endosperm are of various sizes. The number of chromosomes appearing in the division of the primary endosperm cell is larger than that characteristic of the sporophyte (fig. 24).

I. According to Lotsy, fertilization occurs soon after the constitution of the primary endosperm is complete (*cf.* Lotsy [1899] fig. 34).

E. Discussion.

Although there are some important gaps in the preceding account of the origin of the endosperm of *Gnetum africanum*, it is probably safe to assume that the endosperm in this species at least is homologous with that of *Welwitschia*. Taking into account the previous statements of Karsten and Lotsy regarding the development of the endosperm of the species studied by them, there can be little doubt that, except perhaps in the time of its formation, the endosperm of *Gnetum* as a whole resembles that of *Welwitschia*, and that both differ in the particulars described from that of *Ephedra*. Is any morphological importance to be attached to these differences, or not?

In the account previously given of the *Welwitschia* endosperm *, its morphological character was discussed. The conclusion arrived at was that, inasmuch as the nuclei of the primary endosperm cells were formed by the fusion of nuclei of the x-generation which were potentially sexual, and lost their sexuality only as a result of fusion, the endosperm was not a prothallus, but a new structure recognized as a definite morphological entity under the name of "Trophophyte." It was further pointed out that the endosperm of the Angiosperm might perhaps prove to be a more highly specialized form of the

* Pearson, 1909.

trophophyte found in *Welwitschia*. There are therefore two questions concerned here, of which the more comprehensive is that of the relation of the endosperm of *Welwitschia* to that of the Angiosperm. The force of any argument based upon *Welwitschia* alone could not but be diminished by the aberrant character of the genus. It might be urged that the manner in which the endosperm was formed was but a link in a chain of adaptations to peculiar conditions. The occurrence of the same type of endosperm in *Gnetum* is a fact which must be accorded great weight in any view that may be taken.

This interpretation of the *Welwitschia* endosperm has been discussed by Lotsy*. After giving a brief outline of the hypothesis referred to in the last paragraph, the author says:—"Was ist nun der Grund, dass Pearson bei *Welwitschia* die Kerne des Embryosackes, trotzdem sie, ebenso wie bei allen anderen Gymnospermen, aus wiederholter Teilung des Macrosporenkernes entstehen, nicht als Prothalliumkerne sondern als Gametenkerne auffassen will? Der Grund ist

"(*a*) dass die des oberen Teiles befruchtet werden;
"(*b*) die des unteren Teiles miteinander fusionieren können."

With regard to the latter (*b*), Lotsy very truly remarks that it is "kein triftiger Grund." It may be admitted, without further question, that the fact of fusion does not in any way help us to determine the nature of the nuclei which enter into fusion; nor, in fact, was it ever put forward as having any bearing upon the question. These nuclei would have been regarded as gamete-nuclei if they never fused.

The other reason given by Lotsy (*a*), which he describes as "eigentlich nur ein Spiel mit Worten," is more to the point, though, standing by itself, its meaning and force are not clear.

On the previous page† Lotsy admits that "alle Kerne im Embryosack von *Welwitschia* homolog sind." Therefore, if the nuclei of the micropylar region of the sac are gametes, as they undoubtedly are, the free nuclei of the lower region, which normally fuse to form the nuclei of the primary endosperm cells, *may* be sexual also. The reasons for regarding them as sexual, which were given in detail‡, may be repeated here, omitting the first three, since the homology is admitted:—

4. When septation is completed some compartments contain few nuclei (six or less); others a larger number. The latter are normally confined to the lower three-fourths of the sac; the former may occur anywhere, though they usually fill the upper fourth of the sac and are either absent from or much less abundantly developed in the lower three-fourths.
5. In compartments containing less than six, wherever they may be situated, the nuclei do not fuse, but remain free; these are functional gametes. Fusion occurs only in those compartments in which the nuclei are in greater number; a sterile tissue is thus formed.
6. In an abnormal case in which the upward growth of the sac was impeded by a second one above it, compartments which normally would have contained

* Lotsy, 1911, p. 340. † Lotsy, 1911, p. 339. ‡ Pearson, 1909, p. 373.

gametes and produced embryo-sac tubes became uninucleate endosperm cells by nuclear fusion.

7. Under certain circumstances, no endosperm is formed at all, but, with the exception of a few which succumb to the greater activity of their neighbours, all the nuclei remain free and every compartment produces an embryo-sac tube of the normal type.
8. In two cases (Pl. 32. figs. 16, 17) about six gametes in an advanced embryo-sac tube have fused to form a nucleus in all respects like that of a primary endosperm cell.
9. A small tissue found in an embryo-sac tube and consisting of seven cells is interpreted as an endosperm formed by such a nucleus as those referred to in § 8.

It is submitted that, when these grounds are substituted for those given by Dr. Lotsy, it is difficult to avoid the conclusion that the unfused nuclei of the eventually sterile part of the sac are not only homologous with, but also potentially the physiological equivalents of, the functional gametes. They are potential gametes; they cease to be these when they fuse.

The same conclusion for the fusing nuclei of *Gnetum* is founded partly on fact, partly on analogy. But until complete proof is forthcoming, it may reasonably be adopted. It has already been adopted by Coulter and Chamberlain, who write :—" The free nuclei (of the *Gnetum* sac) are potential egg-nuclei, although a group near the antipodal end of the sac may be as distinctly vegetative as are the antipodal cells of Angiosperms " *.

When this nuclear fusion in *Welwitschia* was first described, reference was made to the occurrence of multinucleate cells in the prothallia of other gymnosperms (including *Ephedra*) and to the nuclear fusion which occurs in these cells in *Taxus* †. As Lotsy ‡ appears to regard this fusion as in all respects similar to that which occurs in *Welwitschia*—and now in *Gnetum*—further reference may be made to it.

Multinucleate cells occur in the prothallus in many Conifers §. These may be due either to the formation of multinucleate alveoli or to the occurrence of free nuclear division in uninucleate endosperm cells. In most cases this condition, however attained, is not followed by nuclear fusion. If a multinucleate cell becomes uninucleate, it does so, not by the fusion of its nuclei, but by the formation of new dividing walls; otherwise it remains multinucleate. Saxton, discussing these cases, concludes that " there is no evidence that the (multinucleate) character is of any importance, except as a nutritive adaptation."

There are two conspicuous cases in which the multinucleate condition in the prothallial cells of the lower Gymnosperms is followed by fusion, and they are worthy of attention. In *Ephedra*, Strasburger ‖ states, free nuclear division occurs in the neighbourhood of the archegonia, not only in the endosperm *but also in the nucellus*. The division is

* Coulter and Chamberlain, 1910, p. 388. † Pearson, 1909, p. 356. ‡ Lotsy, 1911, p. 340.

§ Lawson, 1904, 1907, 1909; Saxton, 1909, 1910, 1913; Sinnott, 1913.

‖ Strasburger, 1880, pp. 106, 107.

accompanied by the formation of cell-plates, which, however, do not stretch completely across the cell and are evanescent. Usually there is only one such division in the cell; sometimes a second one follows, producing four free nuclei *. In the nucellar tissue adjacent to the pollen-chamber the cells become disorganized, the nuclei of those which are multinucleate fusing to a "formless mass." The endosperm cells, especially those of the jacket-layer, mostly become binucleate; shortly before the cells are destroyed the nuclei fuse †. In the endosperm cells lying further from the archegonia, an incomplete nuclear fusion occurs not rarely, but here the nuclei entering into fusion do not lose their individuality. The fact that the cells of the nucellus in the region most liable to exhaustion undergo changes similar to those described for similarly situated endosperm cells, leaves little doubt that we are here dealing with degenerating cells. The multiplication of nuclei and their subsequent fusion are nutritive phenomena preceding the destruction of the cell.

Jaeger's ‡ account of the multinucleate cells of the prothallus of *Taxus* is of especial interest, since this is the case particularly referred to by Lotsy. Until June or early July the prothallus is composed of uninucleate cells. Early in July, a month or more *after* fertilization, single cells become binucleate by indirect division; cell-plates are formed, but are of short duration. About the middle of July some of the endosperm cells contain as many as eight free nuclei—these having possibly arisen by direct division. At the end of July cells with sixteen free nuclei are found §. At this stage the nuclei are apparently in perfect condition. About the end of August they show signs of degeneration; they have decreased in size, have lost their spherical form, and have become "unregelmässig, zerrissen, ausgefranst." At the beginning of September the nuclei in the endosperm cells beneath the growing embryo are usually reduced to one, the rest to six or less. These have become further reduced in size and are of indefinite form. Finally, the nuclei in each cell fuse to form 4, 3, or 1 "Kernfleck" ‖. These processes occur first of all in those cells of the endosperm which are contiguous to the archegonia or the embryo. "Das dürfte wohl auf Embryowirkung zurückzuführen sein."

Here also we have a case of tissue-degeneration in which nuclear fusion represents almost the final stage. It will also be noted that both in *Ephedra* and in *Taxus* the multinucleate condition is attained by a cell which was at first uninucleate.

The nuclear fusion which constitutes the primary endosperm cells of *Gnetum* and *Welwitschia* is of a very different character. The multinucleate character of the compartments in which fusion occurs is produced in the primary septation of the sac. Neither it nor the subsequent fusion can be held to be in any way influenced by the activities of a parasitic organ or organism. The fusion is not one of a series of changes leading to degeneration and death; on the contrary, it inaugurates a new phase of growth and subdivision, in the course of which a degree of organization appears in the tissue produced; for not only does it show a well-marked apical growth and regional distribution of nutritive cells ¶, but, in *Gnetum*, a differentiation into "a central region of smaller,

* Jaccard, 1894, p. 34, fig. 48.
† Strasburger, 1880, pp. 106, 107.
‡ Jaeger, 1899.
§ Jaeger, 1899, t. 17. fig. 29.
‖ Jaeger, 1899, t. 17. fig. 30.
¶ Pearson, 1909, p. 370.

more compact cells, and a more extensive peripheral region of larger looser cells" *. In its physiological results it is to be compared with the fusion of the polar nuclei of the Angiosperms, not with the fusions which characterize the degenerating of the endosperm of *Taxus* and of the endosperm and nucellus of *Ephedra*. The former is a fusion which precedes organization; the latter, disorganization.

Those who favour the latter comparison, must at least accept the onus of proving that it is a real one. Lotsy has passed over the difficulties without any reference to them.

Lotsy† would regard each multinucleate compartment of the *Welwitschia* sac—whether its nuclei are destined to function as gametes or, by fusion, to constitute a primary endosperm cell—as homologous with a Coniferous multinucleate alveolus of the "*Sokolowa*-type." If the free nuclei of the latter are potential gametes, this may well be. But the difficulty is that, so far, they are not known to fuse; those of *Welwitschia* and *Gnetum* do. And if the nuclei of the "*Sokolowa*" alveolus did fuse and constitute a cell which divided to form a tissue, would this tissue be gametophytic? In *Taxus* and *Ephedra* the fused nuclei lose one of the most distinctive characters of the generation in whose disorganization they appear, and they leave no descendants.

If, then, the endosperm of *Welwitschia* and *Gnetum* is not merely an adaptation of the fusion of degeneration occurring in a few of the lower Gymnosperms, what is it? It must be a modification of the gametophyte, or of the sporophyte, or something different from both. In discussing this question it is well to bear in mind that no criterion distinguishing the gametophyte from the sporophyte, applicable to all cases, is yet known. But when the life-history includes fertilization, there must be a compensating reduction of chromosomes. Consequently, in such cases the number of the chromosomes is at least a character of importance. The endosperm nuclei in these two genera contain a larger number of chromosomes than even those of the sporophyte. Another character which is always regarded as decisive when fertilization occurs, is that the gametophyte bears the gametes. The endosperm in these genera does not in any sense bear the gametes. Much has been written about the differences between the prefertilization-endosperm of *G. Gnemon* (such as also occurs in *G. africanum* and *Welwitschia*) and the endosperm formed after fertilization in other species of *Gnetum* described by Karsten. But, so far as is known, all species of *Gnetum* resemble *Welwitschia* in this, namely, that the endosperm is not formed until *after* the constitution of the functional gametes. That being so, no great stress can be laid upon the occurrence of fertilization before or after the formation of the primary endosperm. In the cases investigated the endosperm does not bear the gametes, but is itself produced by them‡. For these reasons it is not regarded as a gametophyte.

Some writers on the morphology of the endosperm of the Angiosperms have argued that this tissue, arising normally from the fusion of two or three (sometimes more) nuclei of the *x*-generation, is a monstrous sporophyte §. Some of the reasoning applied to these cases applies also to *Gnetum* and *Welwitschia*. It is true that no male nucleus participates in the fusion of these genera, but it is well known that a sporophyte is

* Coulter, 1908, p. 45.

† Lotsy, 1911.

‡ G. Brown and Sharp, 1911, p. 449.

§ Le Monnier, 1887; Sargant, 1900; East, 1911.

frequently produced by the fusion of gametophyte nuclei of female origin only. The monstrous form of the sporophyte might well be accounted for by the large number of nuclei entering into fusion *.

The third alternative, namely, that the endosperm of *Welwitschia* (and therefore of *Gnetum*) is neither a gametophyte nor a sporophyte, has been suggested †. It was regarded as a distinct morphological entity, appearing for the first time in the higher Gymnosperms and persisting in a highly modified form in the Angiosperms, "a by-product resulting from the fusion of potentially sexual nuclei" and functionally replacing the prothallus of the lower spermophytes.

It is admitted that the evidence for this last view is small, and may prove to be quite inadequate. Except that it seems impossible to refer this endosperm to the gametophyte, it is probably wiser at this stage not to give it a definite morphological label. But the fact that it occurs in *Gnetum*, as well as in *Welwitschia*, still further emphasizes the necessity of recognizing that its morphological importance is not negligible. These are the only genera among living Gymnosperms in which an endosperm constituted in this manner is known to exist. The only other known case of the origin of an endosperm from nuclear fusion is found in the Angiosperms. Since, also, there is a general consensus of opinion that *Welwitschia* and *Gnetum* are nearer to the Angiosperms than are any other living Gymnosperms, the possibility that the peculiar endosperm of the Angiosperms had its origin in a nutritive tissue not essentially different from that of these two genera cannot be overlooked. In the light of present knowlege it is hardly possible to discuss adequately the morphology of the endosperm of the higher group without any reference to that of the Gnetoideæ ‡.

The relationship of the endosperm of *Welwitschia* to that of the Angiosperm has recently been discussed by Samuels §. The author accepts the view that the free nuclei of the Angiosperm sac are phylogenetically related to the free nuclei of the *Welwitschia* sac:—"La formation libre des noyaux dans les Gnétacées est assurément identique à celle qui a lieu chez les Angiospermes." "Il n'existe, à mon avis, aucune différence essentielle entres les produits de fusion du *Welwitschia* et ceux des Angiospermes" ‖. He considers that the prothallus has disappeared both from the upper Gymnosperms and from the Angiosperms ¶, but he does not otherwise pronounce a definite opinion upon the morphology of the endosperm.

Samuels quotes the following expression used in comparing the sacs of *Welwitschia* and *Peperomia* **:—"There is no evidence that the fusing nuclei of *Peperomia* are potential gametes, but they are probably to be regarded as the arrested representatives of nuclei which in earlier forms were potentially sexual." Commenting upon this

* It may be noted here that pro-embryos of the ordinary type are stated to be formed in *Ephedra distachya* by the fusion of nuclei derived from the jacket-cells (Berridge and Sanday, 1907).

† Pearson, 1909. ‡ *Cf.* Coulter, 1911. § Samuels, 1912.

‖ Samuels, 1912, p. 85. A misinterpretation of the use of the word "trophophyte" may here be corrected. The author says (p. 85) that the endosperm of *Welwitschia*, "pour le distinguer des noyaux de l'albumen des Angiospermes, a été appelé par Pearson trophophyte." On the contrary, the term trophophyte was applied to the fusion-product in both *Welwitschia* and the Angiosperm, to distinguish it from the prothallus of the lower Gymnosperm.

¶ Samuels, 1912, pp. 86, 97. ** Pearson, 1909, pp. 378, 379; Samuels, 1912, p. 97.

he writes :—" Comme Pearson n'argumente pas cette assertion, nous ne pouvons comprendre pourquoi il considère les noyaux du sac du *Welwitschia* entrant en fusion, comme noyaux potentiels, ou noyaux en repos, et pourquoi il ne considère pas comme tels les noyaux des Angiospermes." In the case of *Welwitschia* there is some evidence that the nuclei which fuse are potential gametes, for if by chance fusion does not occur in a compartment embedded in the endosperm, its walls may grow out into the nucellus as an embryo-sac tube *. In *Euphorbia virgata* †, in which sixteen free nuclei appear in the sac (megaspore), it is not known that more than one actually retains the power of functioning as a gamete. If the remaining fifteen have lost that power, then they may be described as "the arrested representatives of nuclei which in earlier forms were potentially sexual." Therefore, *Euphorbia virgata* being substituted for *Peperomia*, the opinion expressed in the sentence above quoted is almost identical with that advocated by Dr. Samuels.

Coulter ‡, regarding the endosperm of the Angiosperm as a gametophyte, considers that "conditions in the embryo-sac favour fusions of any free nuclei, in any number and of any origin." This conclusion will probably not be questioned. And that "there is no necessary phylogeny of such a performance" may also be true for this case, but it seems to demand more evidence in support of it than the author has been able to bring together. Before it can be accepted as the whole explanation of the phenomena, it will be necessary to show why a set of different conditions leads also to nuclear fusion in *Gnetum* and in *Welwitschia*, and why this fusion produces physiological results so closely comparable to those achieved in the Angiosperm. It would appear that the intracellular conditions in the multinucleate alveolus of *Cryptomeria japonica* §, for example, are as favourable to nuclear fusion as those which exist in the Angiosperm sac and in the multinucleate compartment of *Gnetum*. And yet fusion does not occur. And if the fusion itself possesses no morphological significance, the phylogeny of the nuclei which fuse is still to be determined. Among the very diverse views that have been entertained, the possibility that the polar nuclei of the Angiosperm may be morphologically (as well as functionally) the representatives of the fusing nuclei of *Welwitschia* and *Gnetum*, has perhaps received too little attention.

While the whole question is involved in much obscurity, it is surely not desirable at the present stage of the enquiry that the search for a primitive type of endosperm, from which that of the Angiosperm may be derived, should cease—which would tend to follow from the assumption that the fusion of the polar nuclei, with or without a sperm nucleus, means nothing more than that they could not do otherwise in the conditions prevailing in the embryo-sac. Widely different as are the views adopted by the many authors who have considered the question, nearly all agree that the phenomenon is one the explanation of which is to be found in phylogeny ‖. There is at least a *prima facie* case for

* Pearson, 1909, p. 365, text-figure.

† When the comparison between *Welwitschia* and *Peperomia* was instituted, Brown's (1908) results were unknown to me. The fact that the *Peperomia* sac represents four spores robs the argument of its cogency. The same applies to *Peneæa* (Stephens, 1909) and *Gunnera* (Samuels, 1912). *Euphorbia virgata* (Dessiatoff, 1911) is free from this objection.

‡ Coulter, 1911. § Lawson, 1904, fig. 23. ‖ *Cf.* Davis, 1904.

attempting to trace the origin of the fusion to a more primitive form, such as that which persists in what are admittedly the highest of the Gymnosperms. Those who think otherwise have not yet stated precisely the grounds upon which their objections are based.

National Botanic Gardens,
Kirstenbosch.

Bibliography.

Beccari, O. 1877.—Della organogenia dei fiori feminei del *Gnetum Gnemon*, L. Nota. Nuovo Giornale Bot. Ital. vii. 91 ; Bot. Zeit. 1877, 342.

Berridge, E. M. 1909.—Fertilization in *Ephedra altissima*. Annals of Botany, xxiii. 509.

—— 1911.—On some Points of Resemblance between Gnetalean and Bennettitean Seeds. The New Phytologist, x. 140.

—— 1912.—The Structure of the Female Strobilus in *Gnetum Gnemon*. Annals of Botany, xxvi. 987.

Berridge, E. M., and E. Sanday. 1907.—Oogenesis and Embryogeny in *Ephedra distachya*. The New Phytologist, vi. 127.

Blume, C. J. 1848.—Rumphia, iv. 2–10, tabb. 174–176.

Bower, F. O. 1882.—The Germination and Embryology of *Gnetum Gnemon*. Q. J. M. S. xxii. 278.

Brown, W. H. 1908.—The Nature of the Embryo-sac of *Peperomia*. Bot. Gaz. xlvi. 445.

Brown, W. H., and L. W. Sharp. 1911.—The Embryo-sac of *Epipactis*. Bot. Gaz. lii. 439.

Coulter, J. M. 1908.—The Embryo-sac and Embryo of *Gnetum Gnemon*. Bot. Gaz. xlvi. 43.

—— 1911.—The Endosperm of the Angiosperms. Bot. Gaz. lii. 380.

Coulter, J. M., and C. J. Chamberlain. 1910.—Morphology of Gymnosperms. Chicago.

Davis, B. M. 1904.—Studies on the Plant Cell. V. sect. iv. Amer. Nat. xxxviii.

Dessiatoff, N. 1911.—Zur Entwickelung des Embryosackes von *Euphorbia virgata*, W. R. Ber. d. Deutsch. Bot. Ges. xxix. 33–39.

East, E. M. 1913.—*Xenia* and the Endosperm of the Angiosperms. Bot. Gaz. lvi. 217.

Goebel, K. 1905.—Organography of Plants, vol. ii. Oxford.

Griffith, W. 1859.—Remarks on *Gnetum*. Trans. Linn. Soc. xxii. 299–312, tt. 55, 56.

Hooker, J. D. 1863.—On *Welwitschia*, a new Genus of Gnetaceæ. Trans. Linn. Soc. xxiv. 1–48, tt. 1–14.

Jaccard, P. 1894.—Recherches embryologiques sur l'*Ephedra helvetica*. Lausanne.

Jaeger, L. 1899.—Beiträge zur Kenntniss der Endospermbildung und zur Embryologie von *Taxus baccata*, L. Flora, lxxxvi. 241.

Karsten, G. 1892—Beitrag zur Entwickelungsgeschichte einiger *Gnetum*-Arten. Bot. Zeit. l. 205.

—— 1893.—Untersuchungen über die Gattung *Gnetum*. I. Beitrag zur systematischen Kenntniss der *Gnetum*-Arten im Sunda Archipel. Ann. Jard. Bot. Buitenzorg, xi. 195.

—— 1893(2).—Zur Entwickelungs-Geschichte der Gattung *Gnetum*. Cohn's Beitr. z. Biol. d. Pflanzen, vi. 337.

Lawson, A. A. 1904.—The Gametophytes, Fertilization, and Embryo of *Cryptomeria japonica*. Annals of Botany, xviii. 417.

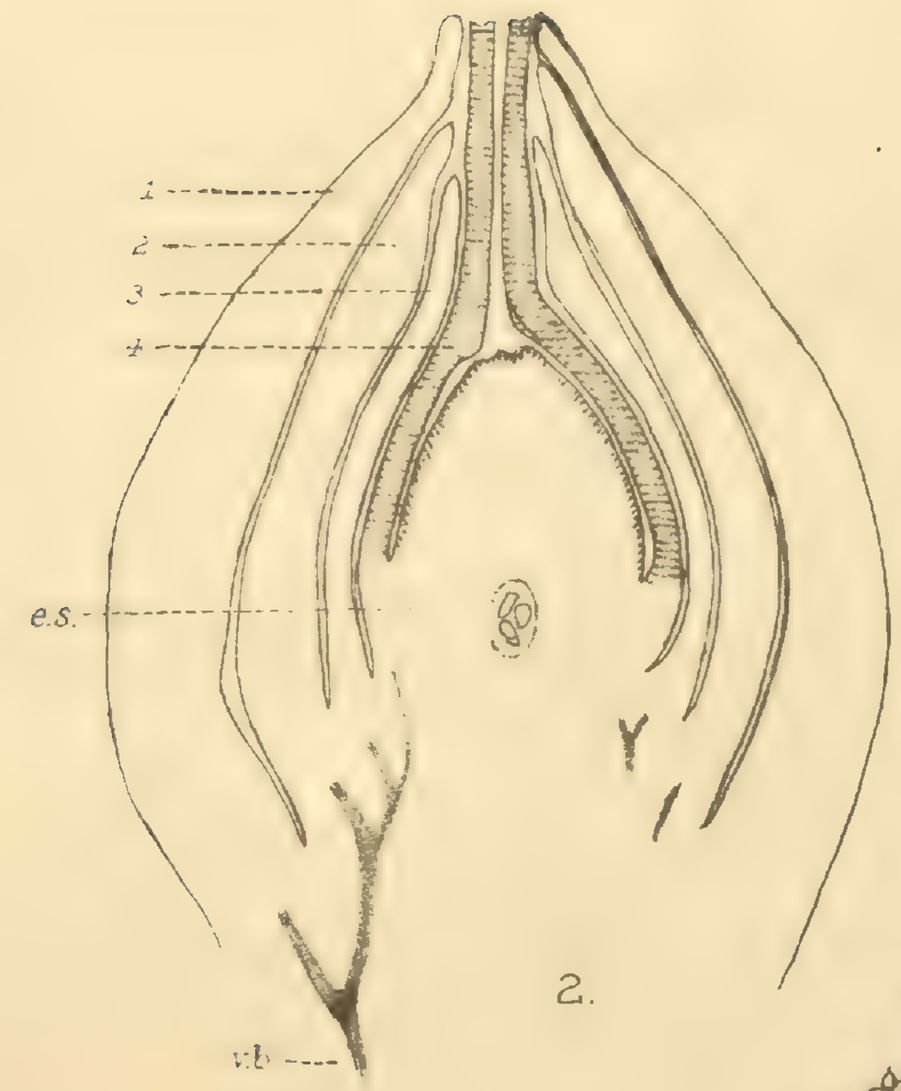
—— 1907.—The Gametophytes and Embryo of the Cupressineæ, with Special Reference to *Libocedrus decurrens*. *L. c.* xxi. 281.

—— 1909.—The Gametophytes and Embryo of *Pseudotsuga Douglasii*. *L. c.* xxiii. 163.

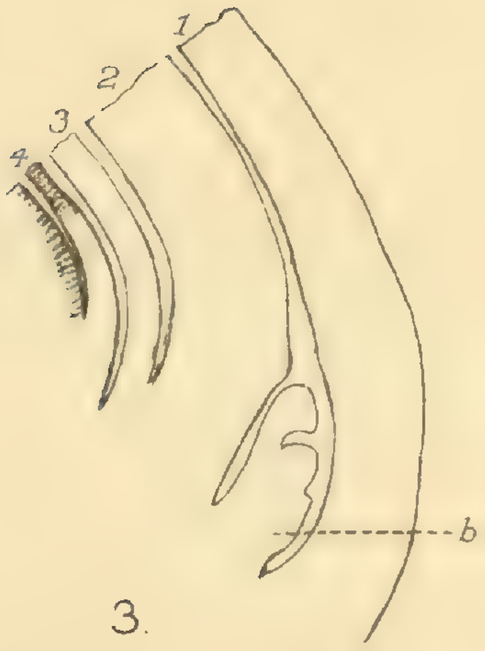
Le Monnier, G. 1887.—Sur la valeur morphologique de l'albumen chez les Angiospermes. Journ. de Botanique, i. 140.

Lignier, O., et A. Tison. 1912.—Les Gnétales, leur Fleurs et leur Position systématiques. Ann. d. Sci. Nat., Bot. 9me sér., viii. 55.

Lotsy, J. P. 1899.—Contributions to the Life-history of the Genus *Gnetum*. I. The Grosser Morphology of Production of *Gnetum Gnemon*, L. Ann. Jard. Bot. Buit. (2) i. 46.

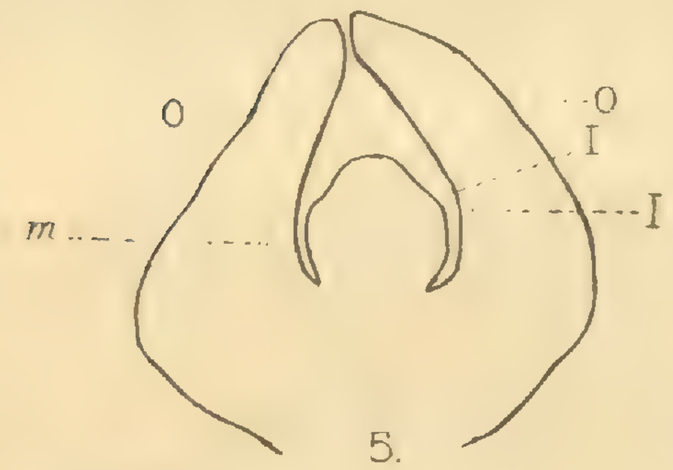


2.



3.

4.

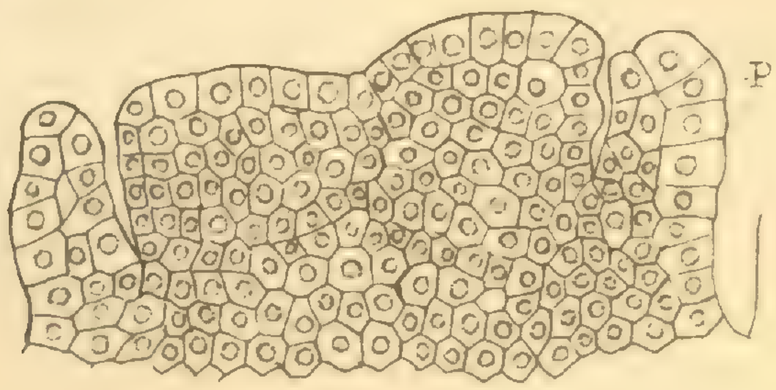


5.

1.

8.

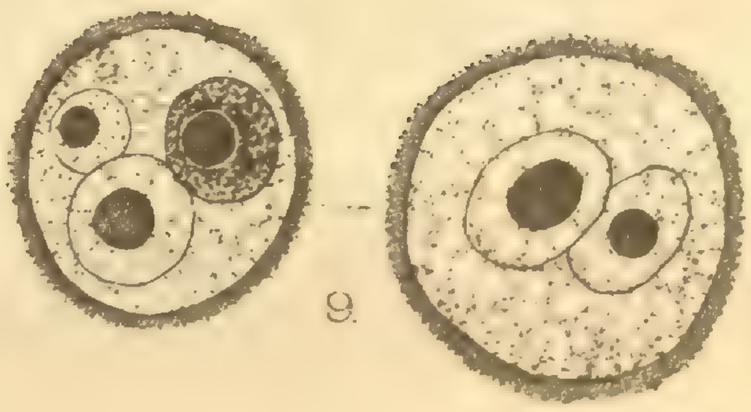
6.



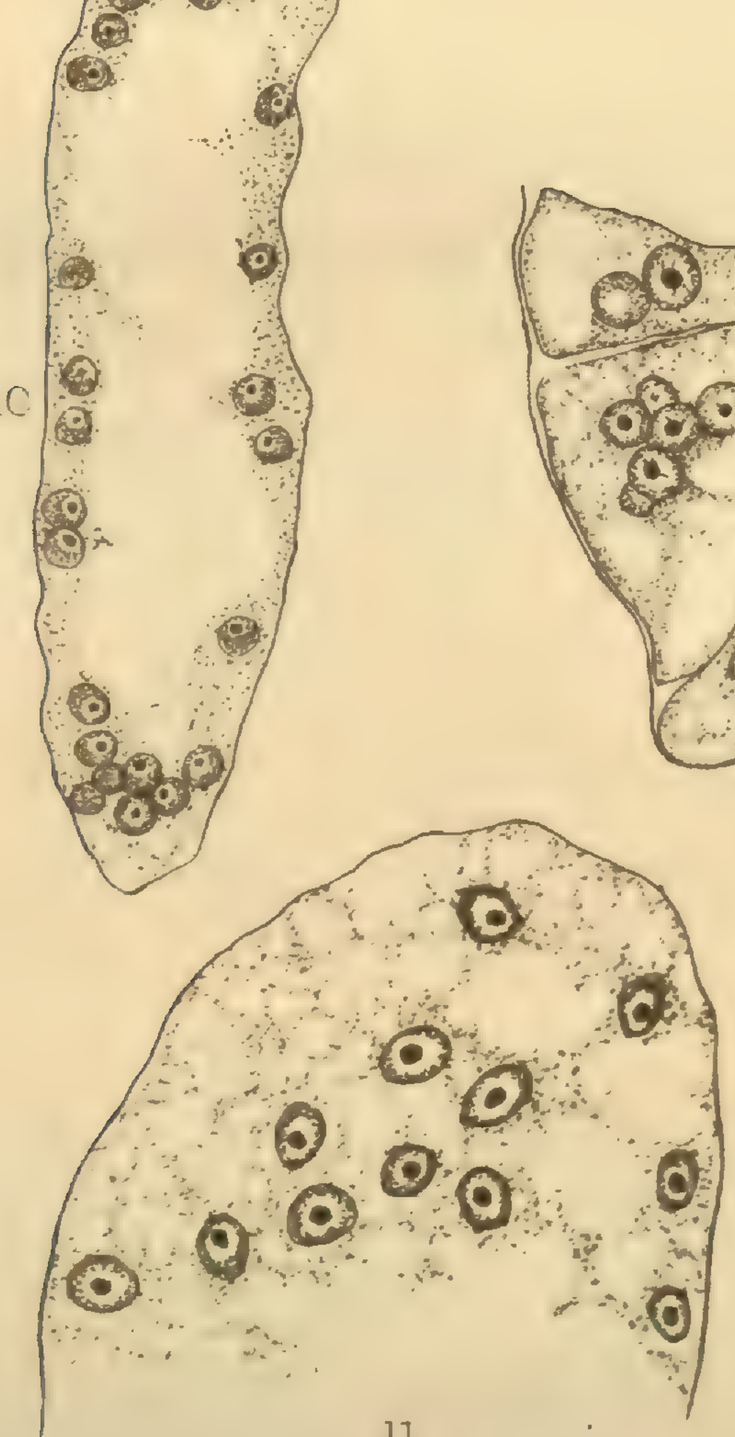
7.

10.

12.

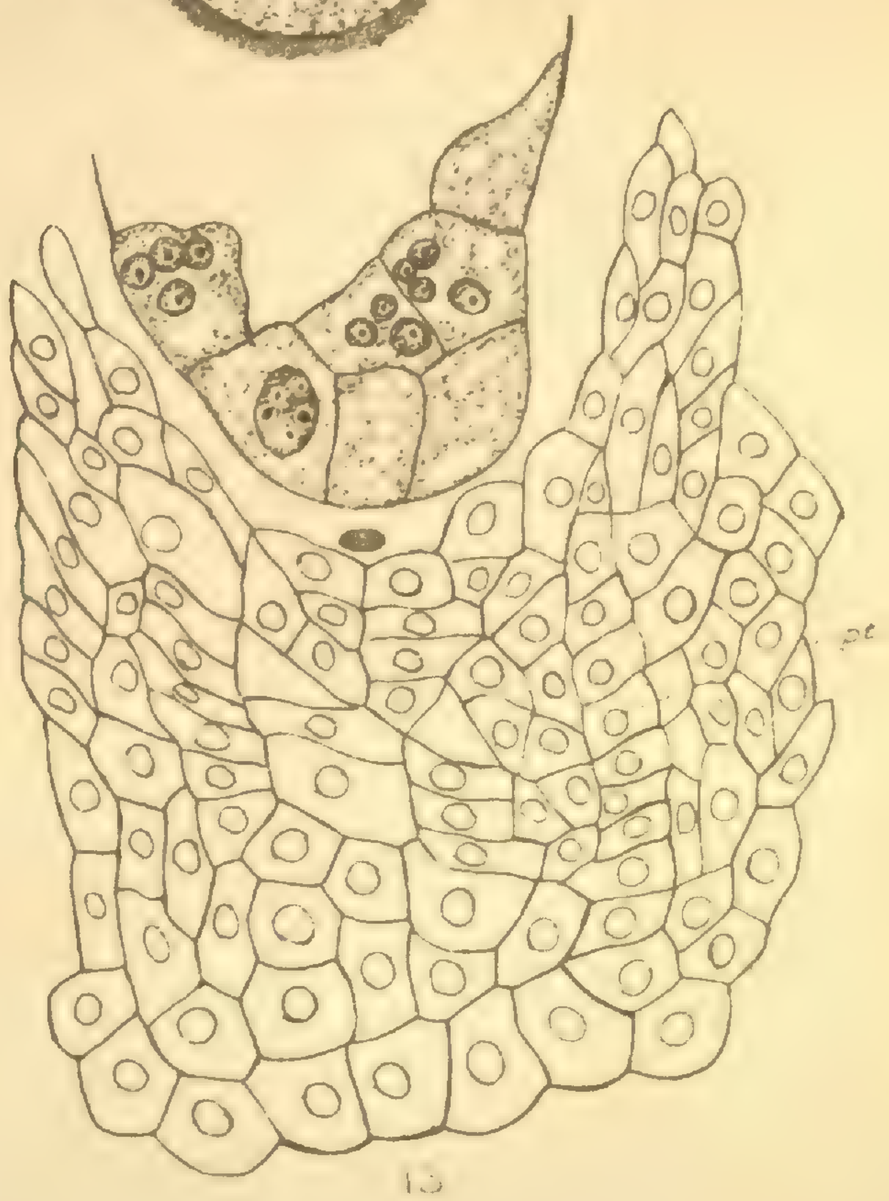


9.



11.

14.



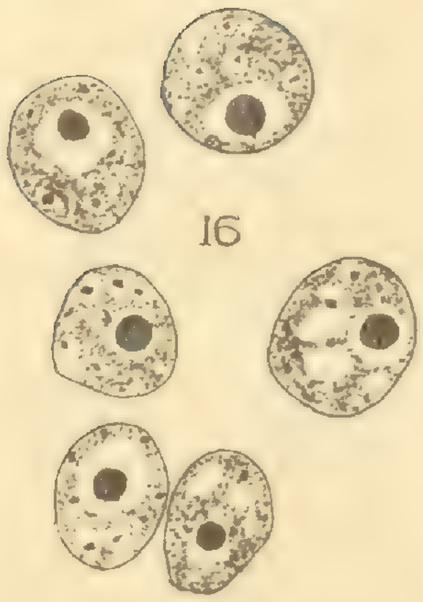
15.

L.B. & H.H.W.P. del.

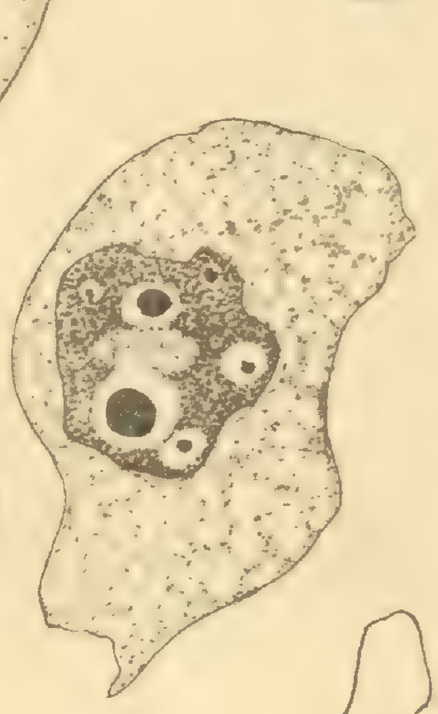
C. Hodges, lith. & imp

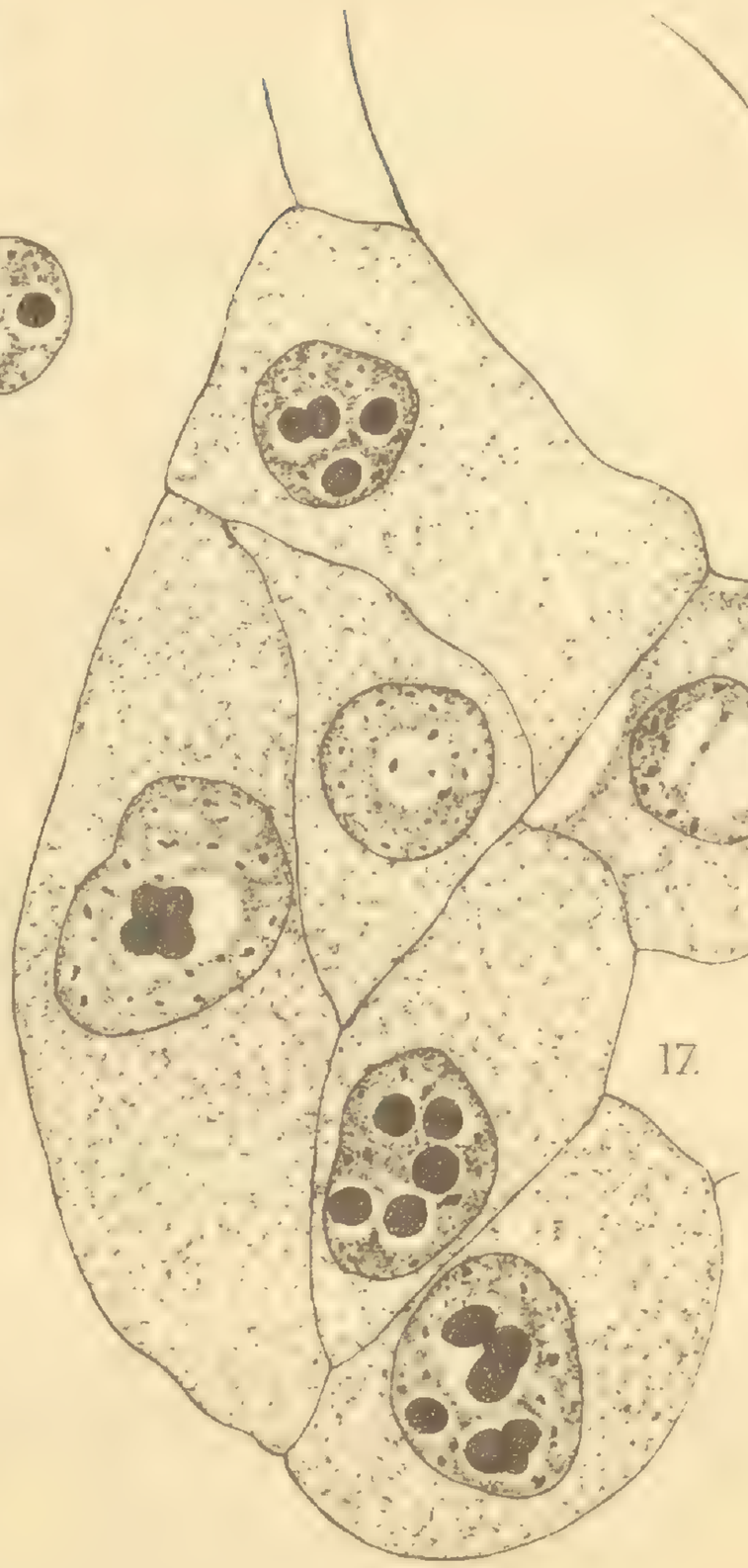
REPRODUCTION IN GNETUM.

15.



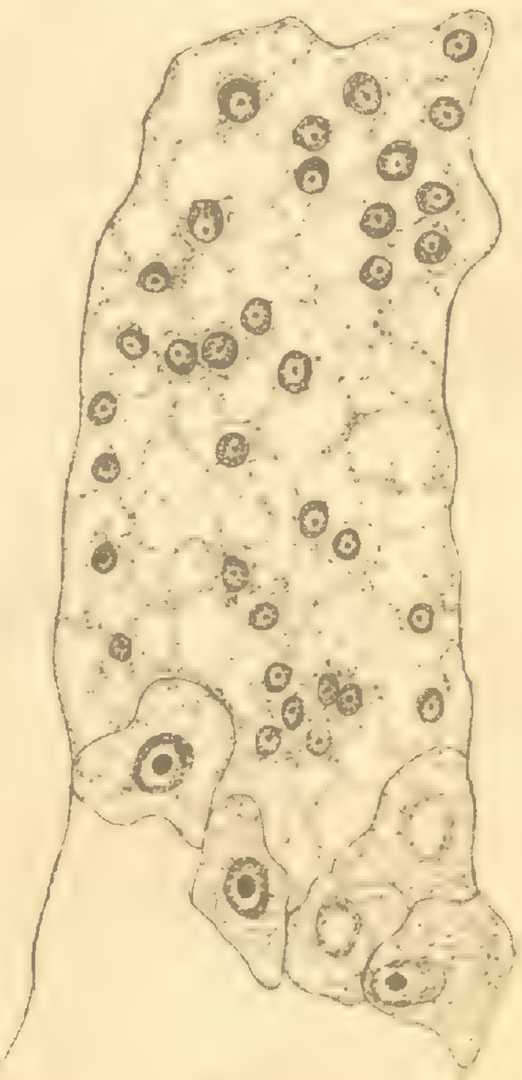
16



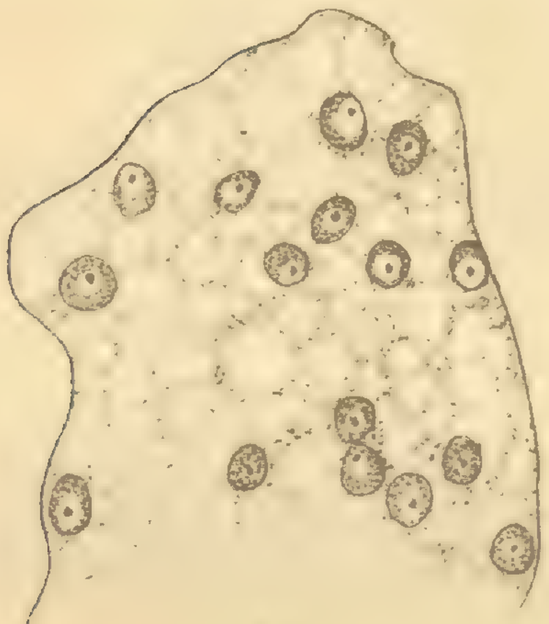


17.

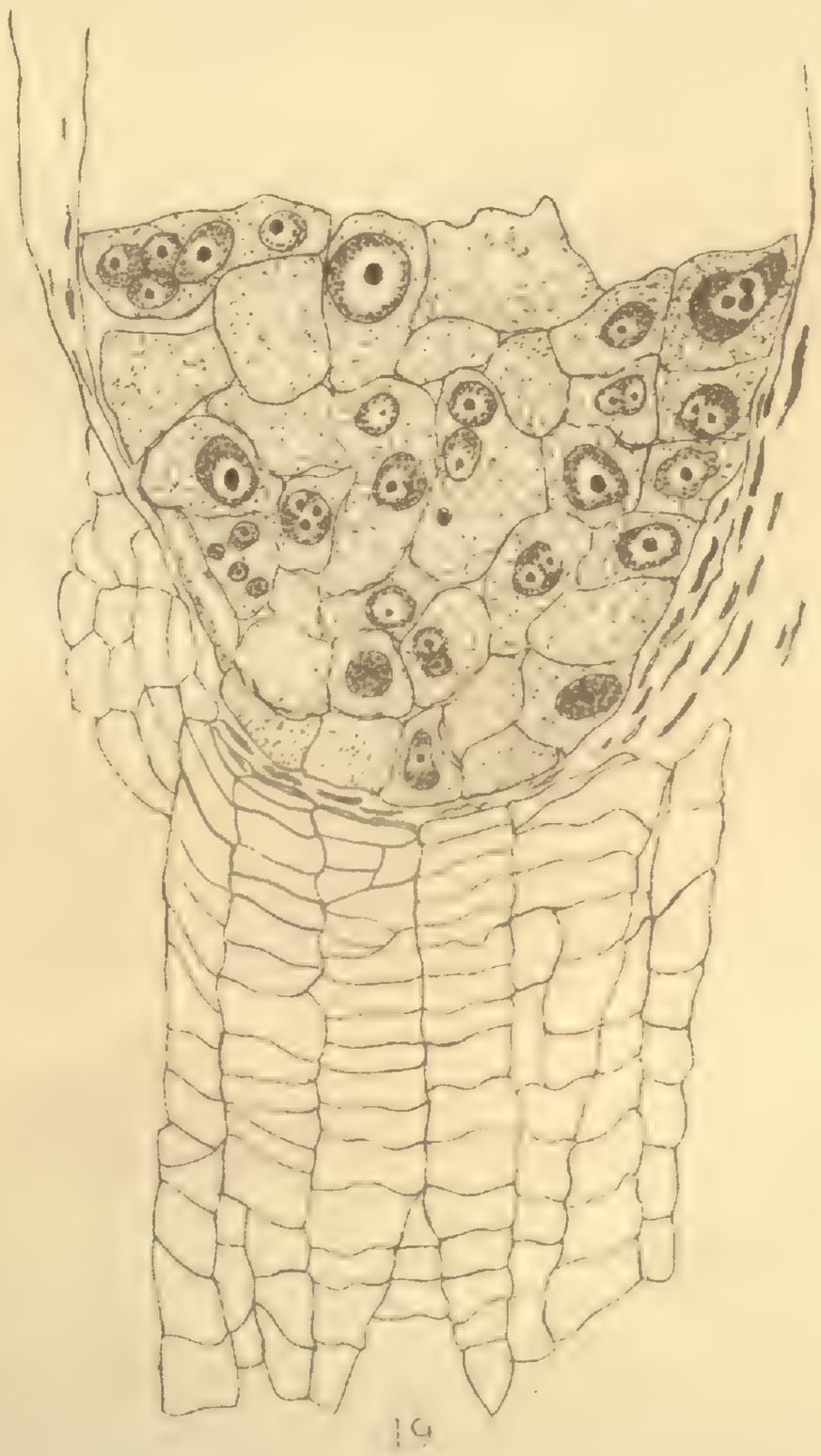
18.

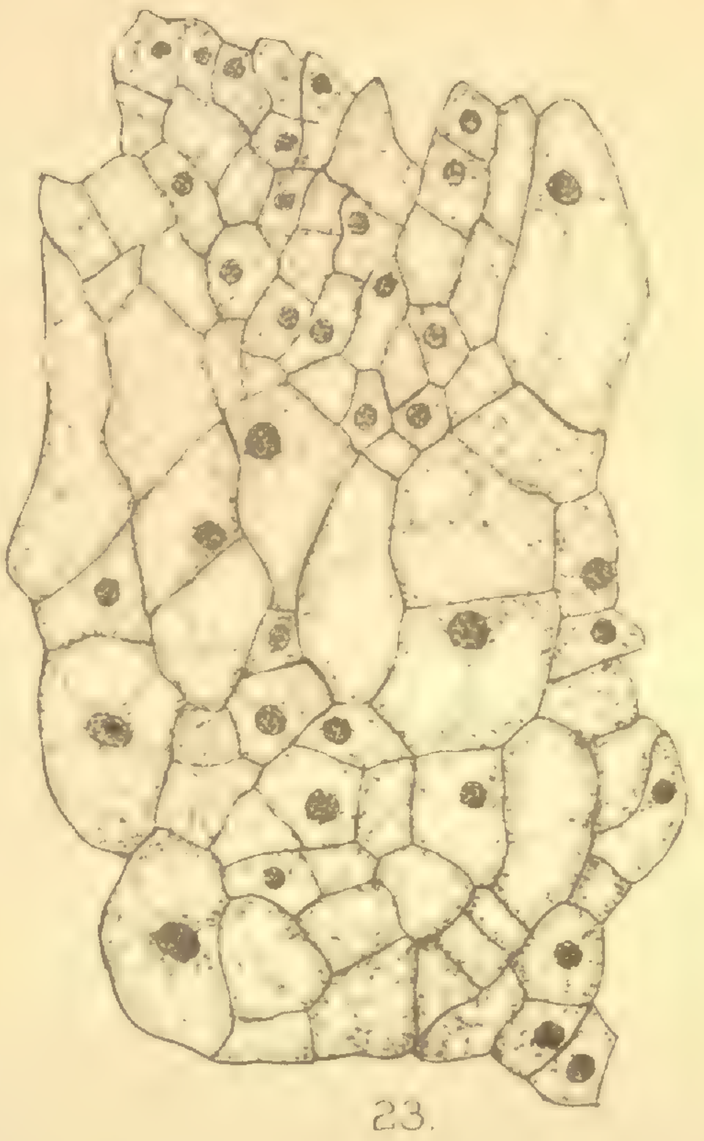


21.



20





23.

22.

19

REPRODUCTION IN GNETUM.

Lotsy, J. P. 1903.—Parthenogenesis bei *Gnetum Ula*, Brongn. Flora, xcii. 397.

—— 1911.—Vorträge über Botanische Stammesgeschichte gehalten an der Reichsuniversität zu Leiden. Ein Lehrbuch der Pflanzensystematik. III. Teil i. Jena.

Pearson, H. H. W. 1906. Some Observations on *Welwitschia mirabilis,* Hook. f. Phil. Trans., B. cxcviii. 265–304, pls. 18–22, figs. 1, 2.

—— 1909.—Further Observations on *Welwitschia*. *L. c.* cc. 331–402, pls. 22–30.

—— 1912.—On the Microsporangium and Microspore of *Gnetum*, with some Notes on the Structure of the Inflorescence. Annals of Botany, xxvi. 603–620, pl. 60, 6 figs.

Porsch, O. 1910.—*Ephedra campylopoda,* C. A. Mey., eine entomophile Gymnosperme. Ber. d. Deutsch. Bot. Ges. xxviii. 40.

Samuels, J. A. 1912.—Etudes sur le développement du sac embryonnaire et sur la fécondation du *Gunnera macrophylla,* Bl. Arch. für Zellforschung, viii. 53.

Sargant, E. 1900.—Recent Work on the Results of Fertilization in Angiosperms. Annals of Botany, xiv. 689.

Saxton, W. T. 1909.—Preliminary Account of the Ovule, Gametophytes, and Embryo of *Widdringtonia cupressoides*. Bot. Gaz. xlviii. 161.

—— 1910. Contributions to the Life-history of *Widdringtonia cupressoides*. *L. c.* l. 31.

—— 1913.—Contributions to the Life-history of *Tetraclinis articulata*, Masters, with some Notes on the Phylogeny of the Cupressoideæ and Callitroideæ. Annals of Botany, xxvii. 577.

—— 1913 (*b*). Contributions to the Life-history of *Actinostrobus pyramidalis,* Miq. *L. c.* xxvii. 322.

Sinnott, E. W. 1913.—The Morphology of the Reproductive Structures in the Podocarpineæ. Annals of Botany, xxvii. 39.

Stephens, E. L. 1909.—The Embryo-sac and Embryo of certain Penæaceæ. Annals of Botany, xxiii. 363.

Strasburger, E. 1872.—Die Coniferen und die Gnetaceen. Leipzig.

—— 1879.—Die Angiospermen und die Gymnospermen. Jena.

—— 1880.—Zellbildung und Zelltheilung. Jena.

Sykes (afterwards Thoday), M. G. 1910.—The Anatomy and Morphology of the Leaves and Inflorescences of *Welwitschia mirabilis*. Phil. Trans., B. cci. 179.

Thoday (formerly Sykes), M. G. 1911.—The Female Inflorescence and Ovules of *Gnetum africanum*, with Notes on *Gnetum scandens*. Annals of Botany, xxv. 1101.

—— 1912. Note on the Inflorescence Axis in *Gnetum*. *L. c.* xxvi. 621.

Tischler, G. 1900.—Untersuchungen über die Entwicklung des Endosperms und der Samenschale von *Corydalis cava*. Verh. d. Naturhist.-medizin. Vereins zu Heidelberg, vi. 351.

Tulasne, 1863, in Martius, Flora Brasiliensis, iv. pars i. t. 103.

—— 1858.—Gnetaceæ Americæ australis. Ann. d. Sci. Nat., Bot. 4me sér., x. 111.

Wettstein, R. von. 1907.—Ueber das Vorkommen zweigeschlechtiger Infloreszenzen bei *Ephedra*. Festschr. d. Naturwiss. Ver. an der Universität Wien, 21–28, tab. 1.

Wieland, G. R. 1908.—Accelerated Cone-growth in *Pinus*. Am. Journ. Sci. xxv. 102.

EXPLANATION OF THE PLATES.

Plate 31.

Figs. 1, 10–23 = *Gnetum africanum*; Figs. 2–9 = *G. Gnemon*.

Fig. 1. Female spike of *G. africanum,* showing aborted ovules and immature ovules and seeds. Natural size.

Fig. 2. Median longitudinal section through an ovule from the lowest node of an androgynous spike of *G. Gnemon*. *v.b.*=vascular system (diagrammatic); *e.s.*=embryo-sacs; 1, 2, 3, 4=envelopes.

Fig. 3. Tangential longitudinal section through the same ovule. N = nucellus; *b* = bud in axil of outer integument. × 300.

Fig. 4. Part of a longitudinal section through the node of the pseudo-androgynous spike, showing an incomplete female flower, two male flowers, and undifferentiated meristem (M). N = nucellus; O = outer, I = inner, *m* = ? middle envelopes of ovule; ♂ = male flower; P = perianth of male flower. × 300.

Fig. 5. Longitudinal section of an incomplete female flower, slightly older than that of fig. 4. O = outer, I = inner, *m* = ? middle envelopes. × 300.

Fig. 6. Longitudinal section of a male flower bearing four anthers. P = perianth. × 70.

Fig. 7. Longitudinal section of a very young male flower. The primordia of the two anthers are indicated. P = ring-like perianth. × 300.

Fig. 8. A four-chambered microspore mother-cell. × 1200.

Fig. 9. Two pollen-grains from the micropyle of a complete flower of an androgynous spike. × 1200.

Fig. 10. A longitudinal section through an embryo-sac of *G. africanum* in the free-nucleate condition. The nuclei at the chalazal end of the sac are crowded. × 300.

Fig. 11. Top micropylar end of the same sac as fig. 12, showing free gamete-nuclei.

Fig. 12. The chalazal end of a later stage of the embryo-sac, showing septation into multinucleate compartments. × 700.

Fig. 13. The chalazal end of an embryo-sac with the underlying nucellar tissue, showing an early stage in the formation of "pavement tissue" (*p.t.*).

Fig. 14. Gamete-nuclei from the micropylar half of an embryo-sac.

Plate 32.

Fig. 15. Three cells from the chalazal end of the same sac as in fig. 14, showing stages in nuclear fusion. × 1200.

Fig. 16. Free gamete-nuclei from the micropylar half of a sac.

Fig. 17. Cells from the upper part of the lower half of the same sac, showing an advanced stage in nuclear fusion, the nucleoli being still unfused. × 1200.

Fig. 18. Outline of a more advanced embryo-sac, showing approximately the division into sterile (*b*) and fertile (*c*) regions. × 70.

Fig. 19. The lower part of the endosperm-tissue of the sac of fig. 18, with a part of the underlying nucellar pavement tissue. In most of the endosperm cells nuclear fusion is proceeding or completed; in a few the nuclei are still free.

Fig. 20. The upper part of the micropylar region of the same sac, showing the irregularly distributed free gamete-nuclei.

Fig. 21. Longitudinal section through micropylar half of a more advanced embryo-sac, showing fertile region with free gamete-nuclei and its junction with the top of the primary endosperm.

Fig. 22. Chalazal end of the same sac, showing almost the whole of the primary endosperm. Except in a few cells, nuclear fusion is complete. × 300.

The pollen-tube has traversed the greater part of the length of the nucellar cap, but has not yet reached the embryo-sac.

Fig. 23. A portion of the endosperm of a more advanced (? fertilized) ovule after the division of some of the primary endosperm cells, showing the very different sizes of the constituent cells (cf. *Welwitschia*, Pearson, 1909, fig. 88). × 300.

X. *On* Isoëtes japonica, *A. Br.*

By Cyril West, *F.L.S.*, *and* H. Takeda, *D.I.C.*

(Plates **33–40** and 20 Text-figures.)

Read 3rd December, 1914.

External Morphology.

Isoëtes japonica, A. Br., which has a fairly wide distribution in Japan, is the largest in habit of any known species of this genus. The caudex * of an old plant often attains a diameter of 4 cm., and, according to Makino (22, p. 146), a diameter of 8 cm. may be reached in very large specimens. The caudex is tri-lobed. In young plants the caudex is sometimes very flat (Pl. **33**. fig. 6), but in older plants, in which it may attain a height of over 3 cm., it appears roughly cylindrical or napiform with three deep longitudinal grooves (Pl. **33**. figs. 4, 7). Except in young specimens, each of the three main lobes of the caudex becomes longitudinally subdivided by a number of very irregular shallow fissures (about half as deep as the main grooves), so that, in transverse section, each lobe appears irregularly incised (Pl. **38**. figs. 56–59). The upper half of the caudex is covered by the 'rosette' of leaves and by the very short leaf-bases. The cells of the latter become slightly thickened and suberized, but they never form a phyllopodium as defined by A. Braun (6, p. 581). The structure designated 'phyllopode' by Makino (*l. c.* pp. 131, 146) is actually the vagina of the leaf.

Along the grooves and fissures the peripheral cells of the cortex also become suberized and form a thin covering of periderm. A similar periderm is formed on the lower surface of the caudex. Numerous roots of a dirty brownish colour anchor the plant firmly in the mud at the bottom of a lake or stream.

Leaves are produced in large numbers; occasionally, more than 200 fully-developed leaves may be counted on a single specimen. These, in plants growing in deep water, attain a length of 1 m. or more. The terminal portion of the leaf is usually aerial and beset with stomata, but leaves which happen to be totally submerged are devoid of stomata.

In transverse section the leaves appear semiterete-quadrangular with the adaxial surface much flattened. The leaf is dilated towards its base, as in all other species of *Isoëtes*, but the wings are comparatively narrow, the width of the vagina at its base never exceeding 2 cm. A few sterile leaves occur on the margin of the leaf-rosette, but the remainder are fertile. In the centre of the rosette of leaves, where a funnel-shaped

* We prefer the term 'caudex' for the structure usually referred to as the 'stem,' 'rhizome,' 'trunk,' or 'stock.'

depression is formed in the caudex, there is a cluster of short immature leaves, which will develop in the following season (Pl. 33. figs. 7, 8; Pl. 34. fig. 10).

It is generally stated (3, p. 34; 6, p. 563; 27, pp. 757–8), that in *Isoëtes* the outermost leaves of the 'rosette' are megasporophylls *, and that these are followed by a cycle of microsporophylls whilst the innermost zone is made up of sterile leaves. This statement, however, is incorrect. In *I. japonica* the sterile leaves, which form the transition from one year's increment to the next, are found on the periphery of the 'rosette.' The mega- and micro-sporophylls are not arranged in any definite order, but are irregularly distributed throughout the wide zone of fertile leaves. When a plant is dug up late in the year, it often happens that the sterile leaves of the outermost whorl of the rosette have by that time completely decayed away; under these circumstances sporophylls are found on the margin. But if such a leaf-rosette be carefully dissected, young sterile leaves will be found in the centre; these are generally regarded as belonging to the present season's growth, but actually they represent the outermost cycle of next year's rosette.

The sporangia are elliptical or narrowly oblong and are embedded in the fovea, the margin of which does not project as a velum.

A well-developed ligule is borne just above the fovea. The ligule is ovate-lanceolate, cordate at the base, and elongate-acuminate towards the apex (Pl. 36. figs. 25, 26, 27, 33). In a small specimen the length of the ligule is about 3 mm., but in a large plant a length of nearly 15 mm. is reached, whilst the width may exceed 5 mm.

Material and Method.

The material used in this investigation was collected near Tôkyô by one of us in September, 1913. Plants of all ages (several weeks to many years old) were represented. The larger specimens were collected from a fairly rapid stream some 3 feet deep, whilst the smaller plants were gathered from narrow ditches where the water was very shallow. All the specimens were preserved in alcohol (about 75 per cent.).

Sections were cut either by microtome or by hand, and were mounted in Canada Balsam or in Glycerine-jelly to which various stains had been added. For the general work we employed the Safranin-Hæmatoxylin combination, but for special purposes several other stains and reagents, including Azo-blue, Corallin-soda, Gentian-violet, Phloroglucin, Chlor-zinc-iodine, Iodine-sulphuric acid, and Sudan III were found useful.

General Anatomy of the Caudex.

We have nothing to add to the existing accounts of the structure and development of the very young sporophyte of *Isoëtes*, the anatomy of which has been carefully studied by Hofmeister (16), Bruchmann (7), Farmer (14), and Campbell (10). The conclusion generally arrived at is that the axile stele of the young sporophyte is made

* Milde (23, p. 275), on the other hand, states that the outermost leaves are microsporophylls.

up entirely of the united basal regions of the leaf- and root-traces. With this explanation of the vascular anatomy of the very young sporophyte we quite agree, but our

Text-fig. 1.

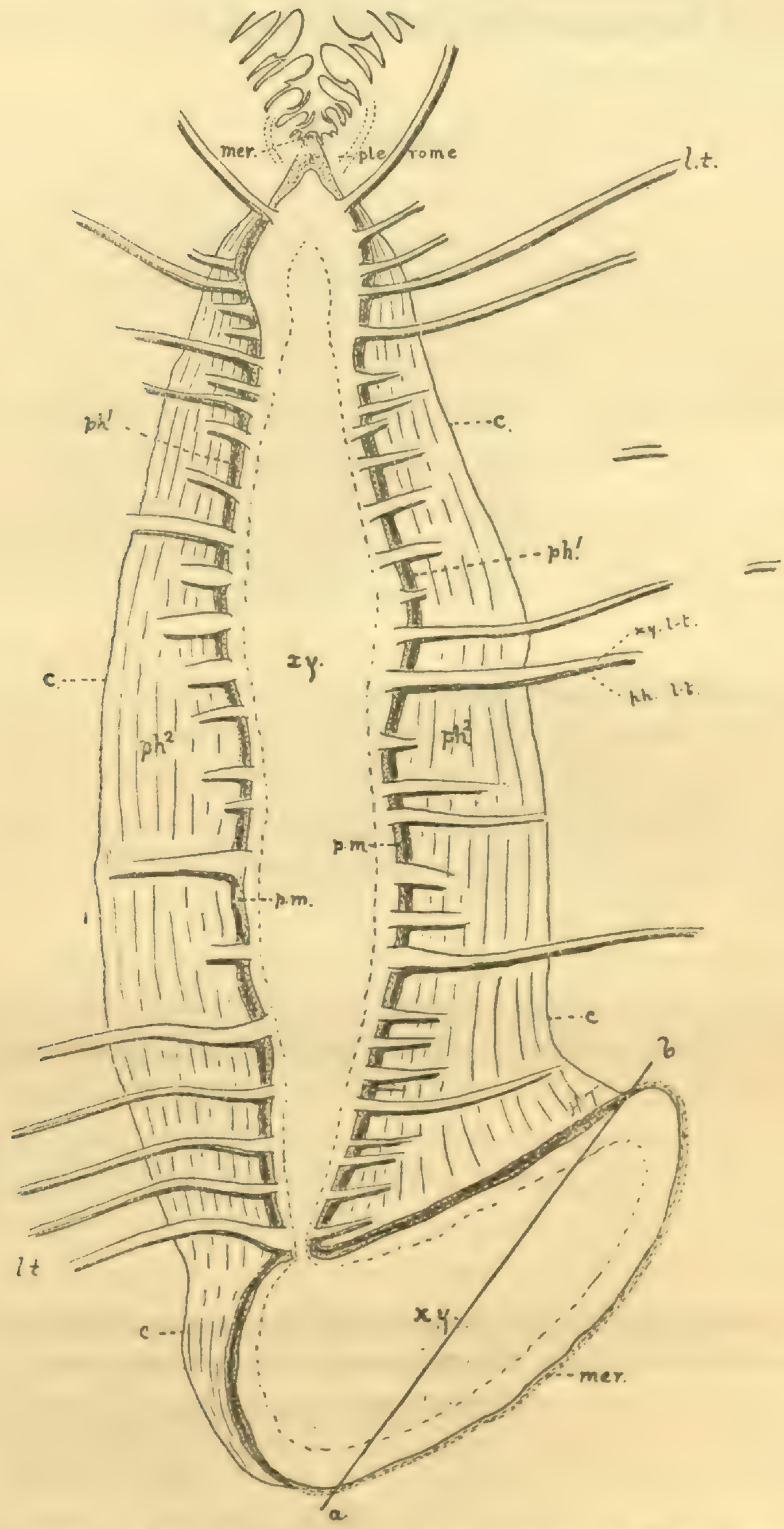


Diagram showing arrangement of primary and secondary stelar tissues of *Isoëtes japonica*. From a median longitudinal section of the caudex cut in the plane of a main furrow. × 20.

c. = cambium. *l.t.* = leaf-trace. *mer.* = primary meristem.
ph.[1] = primary phloem. *ph.*[2] = secondary phloem. *p.m.* = parenchymatous mantle.
xy. = xylem.

investigations have convinced us that the view held by many botanists, who regard the primary vascular cylinder of the adult stem as being made up of a sympodium of leaf-traces, is untenable.

For the reasons given in detail below (p. 338), we have adopted the view already held by Bruchmann (7), Hegelmaier (15), and Scott and Hill (28), that part, at least, of the stele of the adult plant is cauline.

Text-fig. 2.

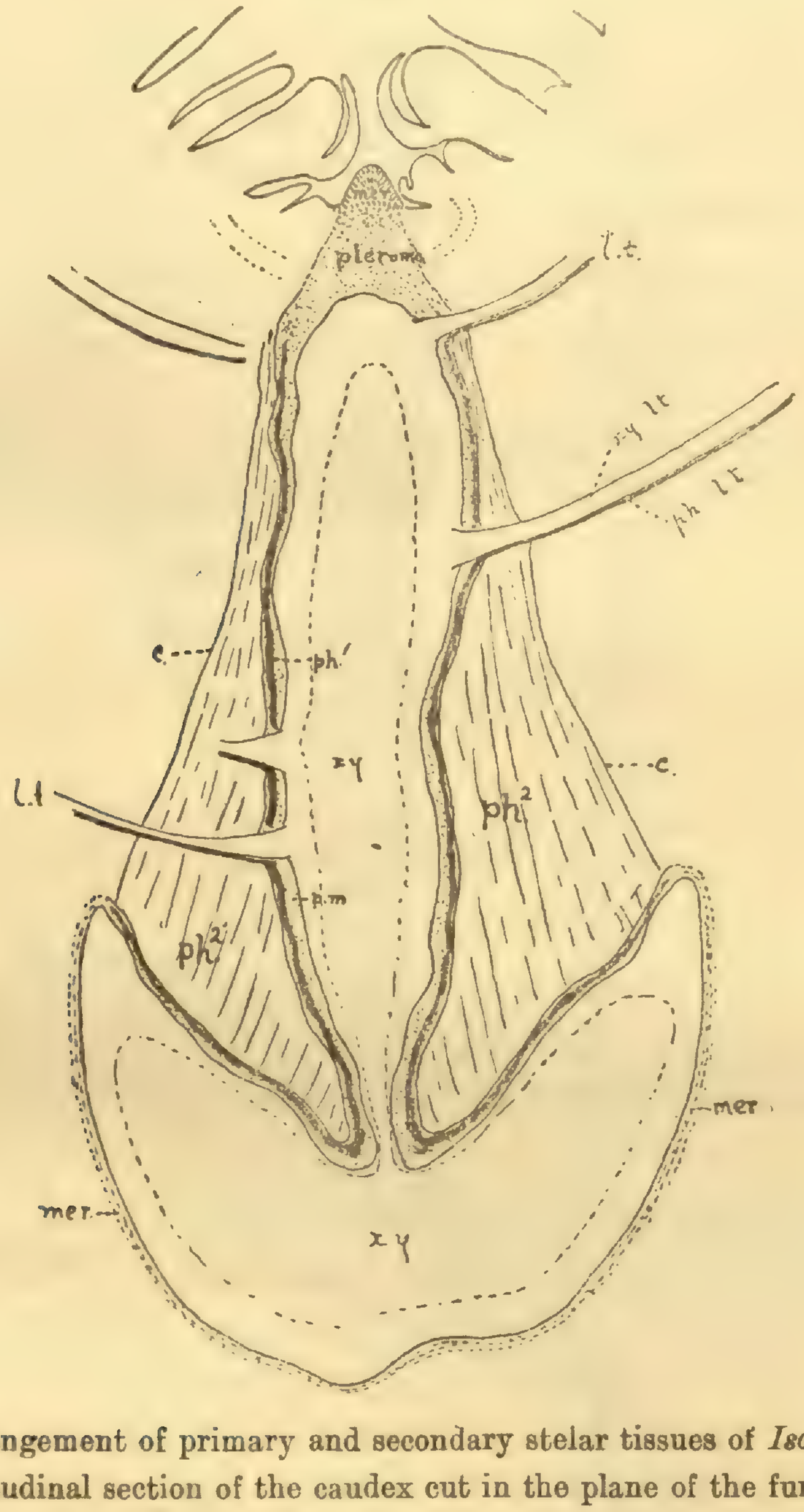


Diagram showing arrangement of primary and secondary stelar tissues of *Isoëtes lacustris*. From a median longitudinal section of the caudex cut in the plane of the furrows. × 50.
(For lettering, see text-fig. 1, p. 335.)

The stele of *Isoëtes* is generally regarded as a single structure (*i. e.* a stem-stele), but we are of the opinion that the stele of the adult sporophyte consists of two distinct parts, namely, a vertical cylindrical portion to which the leaf-traces are confined and which constitutes the stele of the stem proper, and a relatively flattened bi- or tri-lobed basal portion to which all the root-traces are attached (text-figs. 1, 2). The latter we propose to call the rhizophore-stele, since it belongs to a perfectly distinct root-bearing

organ of the plant [*cf.* Lang (20), p. 784], analogous to the swollen basal region of the stem of *Selaginella spinosa* [Bruchmann (8)], or of *Pleuromeia* [Solms-Laubach, (31)].

We assume, however, that owing to its extremely stunted growth, the plant has completely lost all external morphological differentiation into stem and rhizophore.

Apical Meristem and Development of the Primary Tissues of the Stem.

The question as to the exact nature of the apical meristem of the stem of *Isoëtes* has given rise to much discussion in the past.

The first botanist to investigate this problem was Hofmeister (16), who concluded that the tissues of the stem are derived from the segments of a single apical cell, the septa of which are turned towards the furrows of the stem. This apical cell was found at the apex of a blunt cone of cellular tissue situated at the base of the funnel-shaped depression in the upper surface of the cortex (16, pl. li. fig. 4). In arriving at this conclusion, Hofmeister was probably influenced by the prevailing conception of a single apical cell at the apex of the stem of all Vascular Cryptogams.

In the year 1874, this question was discussed in papers by Hegelmaier (15) and Bruchmann (7) respectively. The former maintained that the apical meristem of the stem of *I. velata* and of *I. Durieui* consists of an actual apical-cell surface (Scheitelzellenfläche), and that the cells situated near the centre of this superficial layer of meristem give rise to the mother-cells of the axile woody mass, hence they may be regarded as plerome initials. The more peripheral cells of this meristematic layer, by repeated divisions in an oblique plane, give rise to the primary cortex and to the leaves.

Bruchmann, as a result of his investigations on *I. lacustris*, arrived at a somewhat similar conclusion. He states (7, p. 576), that "Der Stamm wächst durch Urmeristem-Initialen, die anfangs nur aus wenigen Zellen bestehen." In other words, the actual apical meristem is confined to a group of a few cells, which in older plants forms a slight elevation near the centre of the superficial cells of the stem apex. No definite apical cell was observed, but these cells (Urmeristem-Initialen), which may be distinguished from the other superficial cells by their denser protoplasm and by a slight difference in size, divide tangentially, giving rise to an underlying group of meristematic cells, from which both the central mass of xylem and the tissue of the cortex are produced.

In the first edition of his 'Traité de Botanique,' Van Tieghem, referring to the growth of the stem of *Isoëtes*, remarks (33, p. 1294) that "La tige croît, comme celle des Lycopodes, par un groupe de petites cellules mères; mais ici l'on n'observe dans ce groupe aucune differentiation d'initiales propres." But, in a later edition of the same work (34, p. 1429), the following sentence bearing on this subject occurs, "La tige croît, comme celle des Lycopodes, par une seule petite cellule mère."

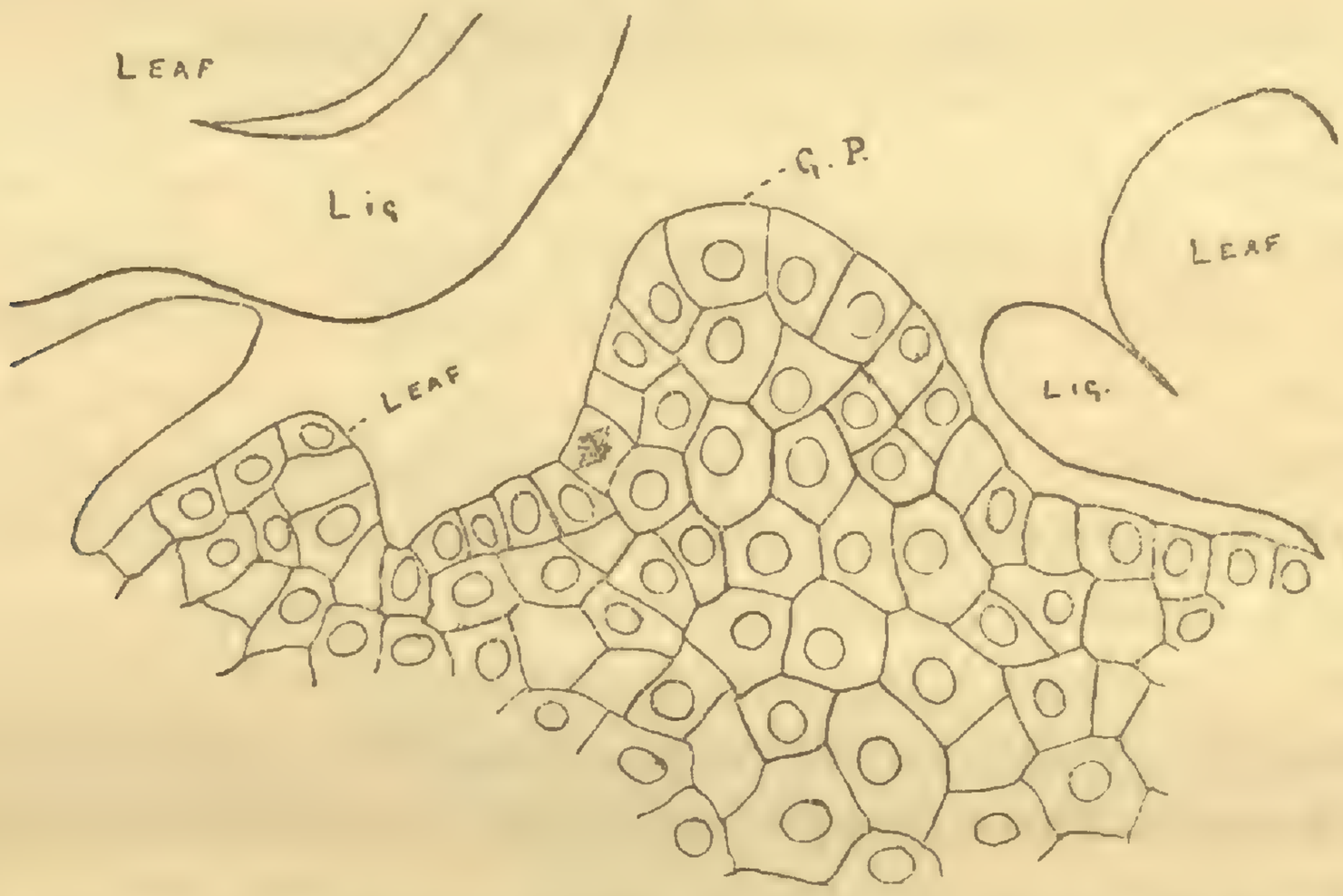
Campbell (10, p. 249) states, in reference to the very young sporophyte, that "the growing-point of the stem . . . . is a nearly flat area, whose surface is nearly at right angles to the axis of the leaf."

Farmer (14) follows Hegelmaier in ascribing to the flat apex of the stem a layer of columnar cells in which most of the divisions are anticlinal, periclinal divisions occurring at rare intervals. The infrequent occurrence of periclinal divisions was correlated with the slow growth in length of the stem in this genus.

A similar conclusion was arrived at by Wilson Smith (30, p. 228), who adds, however, that in longitudinal sections of small plants the stem apex is distinguishable as a slight elevation.

Scott and Hill (28), on the other hand, bring forward, with some reservation, evidence in favour of Hofmeister's original conception of a single apical cell. In our opinion no importance should be attached to the presence of a single cell of slightly larger dimensions than its neighbours, since several large cells can usually be found irregularly distributed over the entire surface of the apical region of the stem. Moreover, these cells often possess a comparatively large nucleus, and may possibly represent leaf-primordia.

Text-fig. 3.



Isoëtes lacustris: longitudinal section through the apex of the stem. The plane of the section corresponds to that of the main furrows. G.P.=growing-point of the stem. × 300.

A careful examination of many series of microtomed sections, both transverse and longitudinal, which were compared with thick hand-sections cleared with potash or 'eau de Javelle,' has revealed the true apex of the stem as a relatively large conical protuberance at the base of the funnel-shaped depression in the centre of the leaf-rosette (text-figs. 1, 2, 3; Pl. 39. figs. 65–72).

We have observed this conical mass of tissue at the apex of the stem of four distinct species, namely, *I. japonica*, *I. lacustris*, *I. Hystrix*, and *I. velata* *; it occurs even in the very youngest specimens of *I. japonica* and of *I. lacustris* which we examined. This protuberance has probably been mistaken for one of the leaf-rudiments to which,

* We are indebted to Prof. J. B. Farmer, F.R.S., for the loan of several slides of the two last-named species.

however, it bears only a very superficial resemblance. Whereas the leaf-rudiments possess a thin layer of cuticle, the conical protuberance which constitutes the apex of the stem has no cuticle.

It is impossible to distinguish any definite apical cell amongst the superficial cells of this protuberance, all of which, as Bruchmann (7, p. 568) correctly observed, are of similar shape and size. These cells usually divide by anticlinal walls, although occasional periclinal divisions are found.

In the underlying tissue ('Urmeristem' of Bruchmann), the cells of which are irregularly arranged, anticlinal and periclinal divisions occur in equal numbers. The relatively large parenchymatous cells lying immediately below the protuberance are arranged in more or less regular series (Pl. **39.** figs. 67, 69, 70) and constitute a poorly defined plerome, the cells of which, probably owing to the peculiar habit of the plant, are not vertically elongated.

Traced still further downwards, a certain number of these large cells are found in all stages of lignification (Pl. **34.** figs. 10, 12). These lignified elements form the tracheids of the stem-stele. Scott and Hill (28, p. 420, Pl. 23. fig. 6) follow Van Tieghem in ascribing a centripetal development to these lignified elements, but in every one of our preparations of *I. japonica* the development of these tracheids is obviously centrifugal (Pl. **34.** fig. 12). It is, perhaps, inadvisable to lay great stress on this point, since a certain amount of irregularity may be expected in such a slow-growing organ.

The remaining cells retain their meristematic condition for a considerable period and ultimately give rise to (1) the numerous small parenchymatous cells (xylem parenchyma), which with the tracheids constitute the xylem of the stem-stele, and (2) a zone of parenchyma which completely surrounds the xylem except where interrupted by the outgoing leaf-traces. This peripheral zone of parenchyma occurs as a definite structure in every species examined; we therefore propose to call it the 'parenchymatous mantle' (text-figs. 1, 2; Pl. **34.** figs. 10, 13; Pl. **38.** fig. 62).

The sieve-tubes of the primary phloem are usually differentiated from the central cells of this zone of parenchyma, in which case they are surrounded both internally and externally by one or more layers of parenchyma (Pl. **34.** figs. 10, 13). But occasionally the more peripheral cells of the parenchymatous mantle become differentiated as sieve-tubes, and since the cambium arises from the outermost layer of the plerome (*i. e.* outermost layer of the 'parenchymatous mantle'), it follows that the sieve-tubes of the primary phloem will then abut directly on the tissues which result from the activity of this cambium (Pl. **35.** fig. 21; Pl. **38.** fig. 64).

We therefore agree with Scott and Hill (28, p. 423) and Stokey (32, p. 320) that the tissue in immediate contact with the primary tracheids is always parenchymatous; as to whether this parenchyma belongs to the xylem rather than to the phloem we prefer to leave an open question, but we usually find that near the apex of the stem the xylem tracheids are differentiated before the sieve-tubes of the primary phloem (text-fig. 1; Pl. **34.** figs. 10, 12).

Possibly this layer of parenchyma, which retains its meristematic activity for a considerable period, was mistaken for a cambium by Scott and Hill (28, Pl. 23. fig. 8).

The primary cortex is formed by the active division of the cells of the apical meristem which abut on the plerome. These cells ($\times\times$ in Pl. 39. figs. 67–69) divide most frequently by oblique anticlinal walls and give rise to parenchymatous tissue which is not sharply marked off from that of the secondary cortex and of the leaf-bases.

Structure of the Primary Tissues of the Stem.

1. *Primary Xylem.*

Stokey (32, p. 314) maintains that "in the short and compact stem there is no indication of a procambial strand, and as there are never any tracheids present above the last leaf-traces the evidences of a cauline portion are not satisfactory." However, neither of these objections will stand the test of a critical examination. Let us consider the first statement that "there is no indication of a procambial strand." In all four species examined by us, a regular arrangement of the meristematic cells lying immediately above the mass of primary xylem tissue was noticed; these meristematic cells form a procambial strand, which is less distinct than that of *Lycopodium*, owing to the fact that in *Isoëtes* the cells are not vertically elongated; this difference may be correlated with the very slow growth of the stem of *Isoëtes* as compared with that of *Lycopodium*. With reference to the second objection, we need only mention the fact that both transverse and longitudinal sections through the apical region of the stem clearly show that the tracheids lying immediately below the procambial strand are fully differentiated before those of any leaf-traces which would connect up with the stem stele at that level (Pl. 34. fig. 12).

Hofmeister (16, p. 356), referring to *Isoëtes lacustris*, states that "many other cells besides the primary cells of the vascular bundles take part in the wood-formation."

Lastly, as further evidence for regarding the stem-stele of the adult *Isoëtes* as a cauline structure, we may mention the fact that the tracheids of the leaf-trace are markedly narrower than, and altogether different in appearance from, those of the stem-stele (Pl. 34. figs. 11, 12; Pl. 35. fig. 21).

Hence it follows that at least part of the central xylem mass of the adult plant represents the xylem belonging to the stem itself. In other words, the adult plant of *Isoëtes japonica* possesses a true cauline stele [*cf.* Scott & Hill (28), p. 426]. The primary xylem-cylinder of the stem of *I. japonica* is composed of numerous large, oval, reticulate tracheids intermixed with abundant xylem parenchyma, the cells of which retain their meristematic condition (Pl. 34. figs. 11, 12; Pl. 40. figs. 75, 78).

The tissues of the primary xylem-cylinder are obviously subjected to a very considerable strain in the horizontal direction, which results in the almost complete disorganization of the tracheidal elements. The cells of the xylem parenchyma, which are capable of further division, are able to accommodate themselves to this pulling strain, and appear healthy even in quite old plants (Pl. 35. fig. 14).

The factors which bring about this result were investigated by Farmer (14), and we cannot do better than quote his explanation, which is entirely confirmed by our own investigations. Farmer (14, p. 41) states that "This result is indirectly brought about by the activity of the cambium. The traces of the roots and leaves which pass through this zone to join the axile vascular cylinder are subjected to great strain by the fact that, whilst the cells round them are growing, and, so to speak, travelling outwards, they themselves are stationary, and can only increase in length by extension. This takes place to a limited extent, and effects a great distortion of their constituent cells, but finally the loose central tissue gives way, and they are partially relieved of the strain at the expense of the cohesion of the inner tissue." Moreover, this explanation accounts for the fact that the pull exerted is in the horizontal direction. In this connection the 'parenchymatous mantle' probably plays an important part. As mentioned above, the primary xylem is completely enveloped by the 'parenchymatous mantle,' which is uninterrupted except by the leaf-traces. The parenchyma of the leaf-traces is connected up with that of the 'parenchymatous mantle,' so that as the leaf-traces are pulled away from the central axis of the stem they drag the 'mantle' with them, with the result that the weaker internal tissues of the stele are compelled to give way. The presence of this parenchymatous mantle also explains the regular outline of the primary tissues of the stele of an adult plant as shown in a median longitudinal section of the stem; if the leaf-traces were connected up directly with the loose internal xylem-parenchyma or with the tracheids of the stem-stele, the outline of the latter would be very irregular (*cf.* text-figs. 1, 2; Pl. 33. fig. 8; Pl. 34. fig. 10).

2. *Primary Phloem.*

The sieve-tubes of the primary phloem have thick cellulose walls, which, in well-stained preparations, show typical sieve-areas. In many of these primary sieve-tubes deposits of callus were observed, and in some cases the deposit was so abundant as to completely fill the cavity of the cell (Pl. 34. fig. 13; Pl. 38. fig. 64).

Primary phloem of a similar character was also found in *Isoëtes lacustris* (Pl. 38. fig. 62).

The sieve-tubes, which are continuous with those of the leaf-traces (Pl. 34. fig. 13; Pl. 35. fig. 15), are associated with unmodified cells of the 'mantle,' several of which contain a semi-transparent substance, which is remarkably resistant to stains. Possibly these parenchymatous cells have a function similar to that of the companion cells of the sieve-tubes of Phanerogams.

The cells of the primary phloem are seldom arranged in regular radial rows, and it is obvious from their arrangement that they cannot have been produced by the activity of the secondary cambium. They are often elongated tangentially (Pl. 34. fig. 13), being subjected to the same horizontal pull as that mentioned above in connection with the primary xylem. The primary phloem of the stem would serve to connect up the phloem of the first-formed leaf-traces with the corresponding tissue of the earlier roots, prior to the formation of the secondary phloem.

3. *Primary Cortex.*

The primary cortex of the youngest specimen examined by us is composed of large parenchymatous cells packed with starch and proteid granules. In the younger part of the plant these cells are isodiametric and form a compact homogeneous tissue, but in the central region of the cortex the cells become loosely arranged with large intercellular spaces. Towards the outer limits of the cortex these cells become collenchymatous, their walls meanwhile increasing in thickness. At this stage the starch-grains suddenly disappear, leaving a loose alveolar mass of protoplasm which has been 'moulded,' so to speak, by the starch-grains before their disappearance. Pl. 38. fig. 60 shows a cortical cell in this condition; numerous proteid granules can still be seen attached to the protoplasmatic framework.

On the margin of the caudex no definite epidermis was observed, but the outermost layers of cortical cells form a rudimentary periderm, the walls of these cells giving the recognized suberin reactions on treatment with Sudan III., etc.

A point of especial interest in connection with *I. japonica* is the presence of an intracellular mycorrhiza in the peripheral cells of the primary cortex. The very fine freely branched non-septate mycelium of the fungus was found in many of these cells. No reproductive bodies of any description were noticed, but the hyphæ formed numerous spherical swellings [vésicules of Janse (18, p. 143, Pl. 13. figs. 7, 8)], either terminally or in an intercalary position (Pl. 38. fig. 61). These swollen portions of the hyphæ contain, at an early stage in their development, a dense granular substance very similar to that found in the hyphæ themselves. The chemical nature of this granular substance was not investigated; it is probably a proteid substance. As these 'vésicules' increase in size they appear to lose their contents, the largest, and therefore, oldest 'vésicules' being quite empty. It is not known why these swellings are produced, but, judging from their wide distribution in the mycorrhiza of several distantly separated groups of plants *, they no doubt possess some unknown but nevertheless important function connected with the nutrition of the fungus or of the host.

Owing to the complete absence of reproductive bodies we were unable to determine the systematic position of this endophytic fungus.

Structure of the Secondary Tissues of the Stem.

1. *Cambium.*

In *Isoëtes japonica* cambial activity starts very early; obvious periclinal divisions in the outermost cells of the 'parenchymatous mantle' were observed in a very young sporophyte, the greatest diameter of the caudex of which measured only 2 mm. The cambium, once formed, persists throughout the life of the plant; more than one cambium in the stem was never observed in our preparations.

* *E. g.*, Marattiaceæ, Ophioglossaceæ [Campbell (11), p. 18], Psilotaceæ [Janse (18), p. 143].

2. *Secondary Phloem.*

The cambium, as stated above, arises very early. It at once begins to cut off new tissues both internally and externally.

Towards the interior the cambium cuts off a tissue the true morphological nature of which has, in the past, provided the subject for much discussion. This tissue consists of compact angular cells more or less regularly arranged in radial rows, and completely surrounds the primary stele of the stem with the exception of the apical region of the latter, forming a zone which is thickest in the oldest (*i. e.* lowest) region of the stem (text-figs. 1, 2).

Considerable interest attaches to this tissue, which is, in many respects, unique in the Vegetable Kingdom.

Von Mohl (24), to whom we owe the first really scientific description of the structure of the genus *Isoëtes*, suggests that the secondary tissue consists entirely of parenchyma.

According to Hofmeister (16) a few spiral cells become added to the wood of old vigorous plants as a result of the cambial activity.

Russow (26), as a result of his anatomical investigations upon herbarium material of several species of *Isoëtes*, arrived at the conclusion that the tissue cut off internally by the cambium consists of parenchyma interspersed with tracheids and with cells which he referred to the phloem.

Hegelmaier (15) refers to this tissue in *I. velata* and in *I. Durieui*, but leaves its morphological nature an open question. He was apparently handicapped by the poor microscopical technique of his day.

Farmer (14) gives a detailed description of the various elements comprising this tissue in *I. lacustris*, but leaves the question of their exact morphological nature undecided.

Wilson Smith (30) considers the adoption of the term 'phloem' inadvisable until further evidence as to the physiological properties of the cells in question is available. He remarks (*l. c.* p. 227) that "no clearly defined sieve-tubes, the essential elements of the phloem, have been found either in the stem or in the leaf." Also, "the inner cells of the prismatic zone are unknown to become secondarily thickened and transformed into xylem tracheids."

Scott and Hill (28), whose investigations were confined to *I. Hystrix*, a terrestrial species, confirmed Russow's original suggestion that this tissue was made up of both xylem and phloem together with a certain amount of parenchymatous tissue.

The most recent description of the secondary tissue of *Isoëtes* is given by Miss Stokey (32), who was fortunate in having material of four different species at her disposal. She maintains (*l. c.* p. 333) that "the so-called 'prismatic layer' is secondary xylem. The cambium does not form phloem." Moreover, she adds that there is no primary phloem in the stem. This conclusion is of special interest, since the four species examined exhibited a very considerable range in habit. That undoubted phloem occurs both in the leaf and in the root, is admitted; if this be so, it is difficult to understand how the products of metabolism can be conveyed from one part of the plant

to another. There is very little evidence in favour of the view that the parenchyma of the secondary cortex takes over the function of phloem. Although it is usual for the xylem of aquatic plants to undergo reduction to a greater or lesser degree, we know of no other genus, either amongst Vascular Cryptogams or amongst Phanerogams, in which the phloem of the stem is reduced to the point of extinction. On the other hand, many aquatics possess a well-developed phloem *.

As a matter of fact, the tissue cut off internally by the cambium is largely composed of sieve-tubes † which are very similar in form to the parenchymatous cells, from which, however, they can easily be distinguished by the presence of definite sieve-areas and frequent deposits of callus and by the absence of starch-grains.

The sieve-areas, which are of the typical cryptogamic type, occur on the radial, tangential, and horizontal walls of the sieve-tubes (Pl. 34. fig. 13; Pl. 35. figs. 18, 19; Pl. 38. fig. 64; Pl. 40. figs. 74, 76); hence it is strange that their presence should have been overlooked or that they should have been mistaken for secondary xylem elements in process of lignification. Many of these sieve-tubes have comparatively thick cell-walls divided by irregular reticulate thickenings into numerous sieve-areas; it is these cells with irregularly thickened walls which appear to have been mistaken for secondary xylem elements by Wilson Smith and by Miss Stokey.

As mentioned above, deposits of callus giving positive reactions to Corallin-soda and other recognized 'callus' stains are very frequently met with in these cells (Pl. 35. figs. 18, 19). Occasionally this substance is deposited in such quantity as to completely fill the lumen of the cell (Pl. 40. figs. 74, 76), especially in the sieve-tubes first cut off by the cambium. A small nucleus is sometimes found in these elements, but, when present, the nucleus is always much smaller than the nuclei of neighbouring parenchymatous cells and is probably undergoing degeneration. Thus, it is evident that the sieve-tubes of the secondary phloem of *Isoëtes japonica* are essentially similar in structure to those found in other Vascular Cryptogams, differing only in shape from the usual type. It has already been shown by Seward and Ford (29) that the so-called 'quergestreckte Zellen' of Zenetti (37), which occur in the stem of *Osmunda* and *Todea*, are actually sieve-tubes, which are considerably elongated in the horizontal (*i.e.* tangential) direction. The description of these peculiar cells given by Seward and Ford (*l. c.* p. 245 and Pl. 29. fig. 40) would serve equally well for the sieve-tubes of *Isoëtes*. Moreover, these authors (*l. c.* p. 242) remark that in the apical region of the stem of *Todea* these cells contain large nuclei.

We have invariably found that on the phloem (*i.e.* lower or abaxial) side of the leaf-trace the sieve-tubes of the secondary tissue are in direct organic connection with those of the leaf-trace, as is clearly shown in Pl. 35. fig. 21. Moreover, a gradual transition from the extremely short sieve-tubes of the secondary phloem to the

* E. g., *Potamogeton*, *Ceratophyllum*, *Elodea*, etc.

† Strictly speaking, these elements are sieve-*cells* and differ from the sieve-tubes of the leaf- and root-traces, which consist of rows of cells (= 'members' of De Bary, 12, p. 172).

more elongated sieve-tubes of the leaf-traces was observed. The sieve-tubes of the basal region of the leaf-traces are remarkably short considering the length of the leaves themselves.

A possible explanation of the peculiar form of the sieve-tubes of the secondary phloem of *Isoëtes* may be deduced from the very slow stunted growth of this plant. It is generally agreed that some sort of correlation exists between the actual rate of growth of a plant-structure and the length of its individual conducting elements. Numerous examples of this correlation might be given; for instance, the segments or members of the sieve-tubes of certain tropical lianes attain a length of more than 2 mm. (e. g. *Calamus Rotang*; *Bignonia* spp., etc.).

Isoëtes lacustris was examined for comparison with *I. japonica*. Short, box-like sieve-tubes, similar in every respect to those described above, were found in the internal secondary tissue (Pl. 35. fig. 20) associated with starch-containing parenchymatous cells and with secondary xylem elements. In this species also, the sieve-tubes of the secondary tissue are in organic connection with those of the leaf-traces (Pl. 35. fig. 16).

In *I. japonica* the parenchymatous cells (*i. e.* phloem-parenchyma) cut off internally by the cambium can easily be recognized by the presence of a relatively large nucleus and numerous starch-grains. The cells labelled *ph.p.* in Pl. 38. fig. 64 are of this nature, although at first sight they might easily be mistaken for the actual cambial cells; the latter, however, as previously pointed out by Scott and Hill (28, p. 424), do not contain starch-grains.

These parenchymatous cells are slightly less numerous than the sieve-tubes; they are always irregularly distributed through the secondary tissue, and, even in very old specimens, are never arranged in definite zones, as described for several other species of *Isoëtes* by Hegelmaier (15, p. 501), Farmer (14, p. 42), and Stokey (32, p. 323). Since the secondary tissue completely envelopes the primary stele, it follows that the cells of the secondary tissue come into contact with the tissues of the leaf-trace as it passes out from the central mass of primary tissue. On the xylem (*i. e.* upper or adaxial) side of the trace a number of parenchymatous cells occur, and these, as already described, connect up directly with those of the 'parenchymatous mantle.'

3. *Secondary Xylem.*

No secondary xylem was found in *I. japonica*; apparently it does not occur in this species, since plants of all ages were examined. Secondary xylem has been described in several other species of *Isoëtes*, namely:—

I. lacustris (Hofmeister, 16, p. 361; Russow, 26, p. 139);
I. Durieui (Hegelmaier, 15, p. 504);
I. Hystrix (Scott and Hill, 28, p. 421);
I. echinospora and *I. Engelmanni* (Wilson Smith, 30, p. 227);
I. Nuttallii and *I. melanopoda* (Stokey, 32, p. 326).

In *Isoëtes lacustris* xylem elements occur spasmodically throughout the secondary

tissues of the stem-stele. These secondary tracheids are very similar to those of the primary xylem and usually occur in groups (Pl. 38. fig. 62), although single elements are occasionally found. The reticulate thickenings of the walls of these elements are lignified; hence, in sections stained with the Safranin-Hæmatoxylin combination, they stand out sharply from the surrounding secondary tissues, which consist of sieve-tubes and parenchyma. Moreover, these secondary xylem elements have no contents.

4. *Secondary Cortex.*

It is generally agreed that the tissue cut off externally by the cambium consists, in all the species of *Isoëtes* hitherto examined, of typical parenchymatous cells, which form the relatively bulky secondary cortex. These cells, which are produced very rapidly, are at first arranged in radial rows and form a compact homogeneous tissue. But, sooner or later, as they move farther and farther away from the centre of the stem, their arrangement becomes correspondingly less and less regular, whilst large intercellular spaces appear between them. These cells contain numerous starch-grains and proteid granules, but oil-drops were never observed.

The walls of the peripheral cells of the secondary cortex become suberized and form a feebly developed periderm.

It is somewhat difficult, even in young specimens, to distinguish the cells of the primary cortex from the parenchymatous cells formed by cambial activity, since they show a general agreement in size, shape, and contents.

Apical Meristem and Development of the Primary Tissues of the Rhizophore.

The results obtained by us from a careful study of the rhizophore region of the caudex of *I. japonica* and of *I. lacustris*, cannot be reconciled with the conclusion arrived at by Scott and Hill with reference to the development of the same region of *I. Hystrix*. These botanists (28, p. 431) give the following explanation of the mode of growth of the rhizophore: "the downward growth of the base of the stem is entirely due to the activity of the cambium, and to the addition of new root-bases." And (*l. c.* p. 441), "The wood, which is added at the bottom of the stele, and which remains functional when the primary wood higher up is disorganised, is entirely built up by the sympodium of root-bases."

It has already been shown that growth of the stem-stele of *I. japonica* is acropetal, fresh xylem and phloem-tissue being added continuously by the slow and gradual differentiation of large plerome cells derived from the apical meristem. The growth of the rhizophore-stele takes place in much the same way; that is to say, the growth of the rhizophore-stele is also acropetal, fresh xylem and phloem-tissue being gradually differentiated from the primary meristem *, which, however, differs from that of the

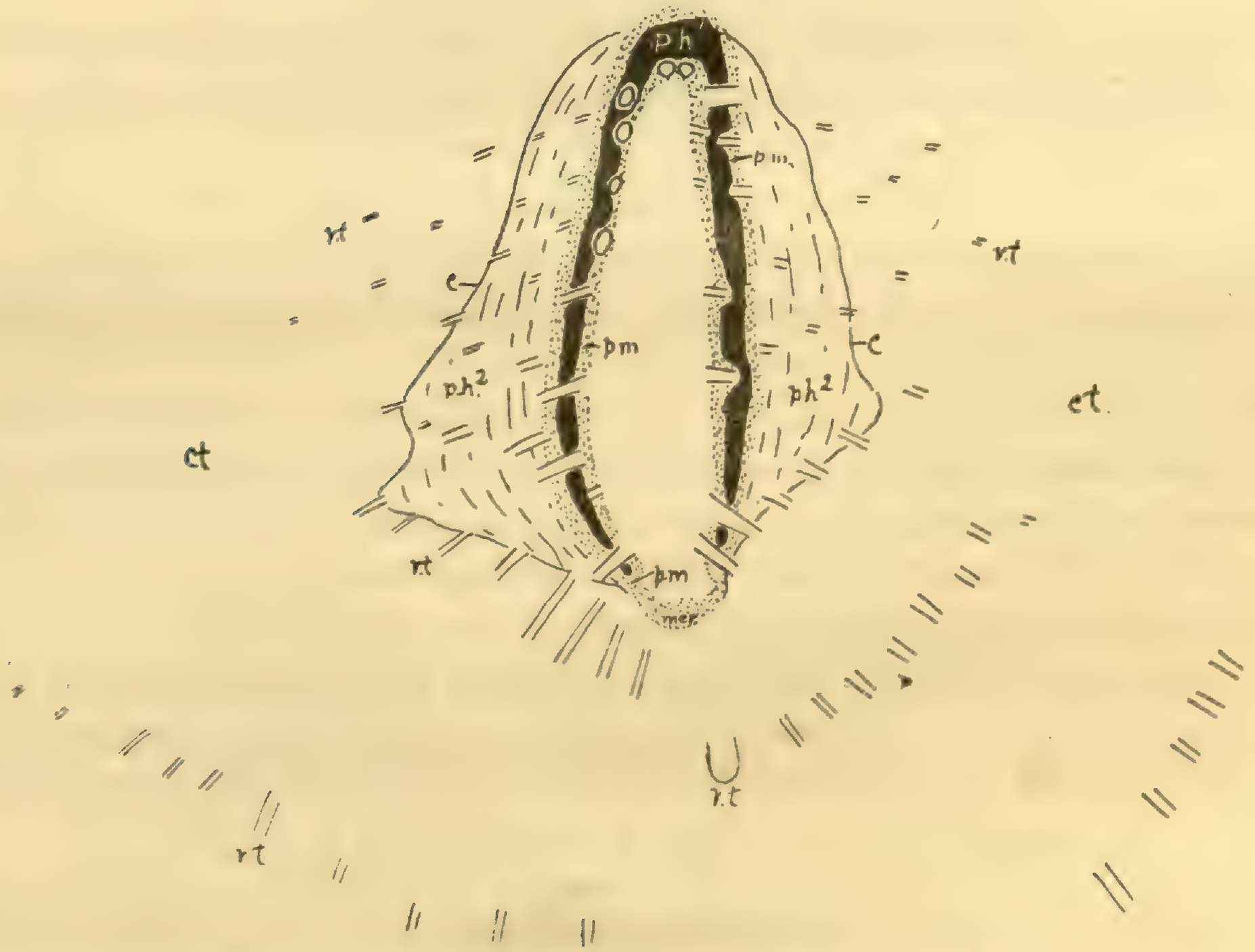
* This meristematic tissue may possibly be regarded as a part of the cambium; but it is present in the embryonic plant (*cf.* Hofmeister, 16, Taf. 48. fig. 3), persists throughout the life of the plant, and is quite distinct both in origin and in appearance from the true cambium. It therefore seemed advisable to distinguish between the two tissues; the term 'primary meristem' is therefore employed with reference to the former.

Text-fig. 4.

Isoëtes japonica. Diagram showing arrangement of primary and secondary stelar tissues. From a transverse section of one of the lobes of the rhizophore-stele. × 20.

c. = cambium. *mer.* = primary meristem. *p.m.* = ' parenchymatous mantle.'
ct. = cortex. *ph.*^{1}, *ph.*^{2} = primary, secondary phloem. *r.t.* = root-trace.

Text-fig. 5.



Ditto: but from an oblique transverse section of a stelar lobe cut in the plane indicated by the line *a*–*b* of text-fig. 1. × 20.

stem-stele in several important details. For instance, the apical meristem of the rhizophore is distributed over a much larger area, since it extends along the whole length of the curved lower edge of each of the three lobes of the stele as indicated in text-figs. 1, 4, 5.

However, it must be remembered that this primary meristem is confined to a very narrow strip of tissue and is completely absent from the lateral surfaces of the stelar lobes. This is clearly shown in text-figs. 4 and 5, which indicate in a diagrammatic manner the arrangement and distribution of the various structures met with in transverse sections through one of the lobes of the rhizophore-stele. Pl. 40. fig. 77 is reproduced from an untouched photo-micrograph of a transverse section through a similar lobe, cut near its apex. In this figure, only those tissues which are found along the lower margin of the lobe are shown. From the central region of this primary meristem the tracheids and parenchyma of the xylem are slowly differentiated (Pl. 39. fig. 63; Pl. 40. figs. 75, 77, and text-figs. 4, 5; also *cf.* Hofmeister, 16, Taf. 52. fig. 6). This results in the continual addition of xylem elements to the primary stele of the rhizophore. From the more peripheral regions of this meristem the 'parenchymatous mantle,' primary phloem, and cambium of the rhizophore-stele are produced (text-figs. 4, 5).

The primary meristematic tissue extends to a point slightly beyond the apex of the stelar lobe, so that the 'parenchymatous mantle' and primary phloem are found along the upper surface as well as on both flanks of the lobe (text-figs. 1, 4, 5). Consequently, the actual growth of the primary tissues of the rhizophore-stele is confined to three radiating lines (*a*, *b*, *c*, in text-fig. 10) separated from one another by an angle of 120° and inclined at an angle of approximately 80° to the vertical axis of the plant (text-figs. 1, 11). Hence, there can be no lateral growth of the primary tissues of the stelar lobes of the rhizophore, and consequently no lateral increase in dimensions apart from that brought about by the extension of tissues already formed. However, the primary tissues of the rhizophore-stele are subjected to a pulling strain by the out-going root-traces (Pl. 40. fig. 80, and text-figs. 4, 5).

The primary meristem of the rhizophore is situated not at the actual periphery of the caudex, as in the stem apex, but is separated from the exterior by several regularly arranged layers of parenchymatous cells (Pl. 38. fig. 63; Pl. 40. figs. 75, 77), which contain numerous large starch-grains. These cells (=primary cortex of the rhizophore) form a structure in many respects analogous to a 'root-cap.'

Isoëtes lacustris was examined for comparison with the above, from which it differs only in the possession of two, instead of three, lobes to the rhizophore-stele.

Structure of the Primary Tissues of the Rhizophore.

1. *Primary Xylem.*

The tracheids of the rhizophore-stele differ both in shape and size from those of the stem-stele. The former are not oval in shape but are considerably elongated (Pl. 38. fig. 63; Pl. 40. figs. 75, 77); they are rather smaller than the tracheids of the stem-stele and are spirally or reticulately thickened.

2. *Primary Phloem.*

The primary phloem of the rhizophore-stele consists of sieve-tubes which are essentially similar to those of the primary phloem of the stem ; they are accompanied by unmodified cells of the 'parenchymatous mantle,' which may possibly constitute the phloem-parenchyma.

3. *Primary Cortex.*

The primary cortex of the rhizophore region needs no further description.

Structure of the Secondary Tissues of the Rhizophore.

1. *The Cambium.*

In the rhizophore cambial activity starts very early, the cambium arising from the peripheral cells of the 'parenchymatous mantle' just below the apical meristem (text-figs. 4 & 5).

2. *Secondary Phloem.*

The tissue cut off internally by the cambium consists of parenchyma and sieve-tubes, which are exactly similar to those of the secondary phloem of the stem.

3. *Secondary Cortex.*

The greater part of the caudex of *Isoëtes* consists of secondary cortex, derived partly from the cambium of the stem and partly from the cambium of the rhizophore.

The secondary cortex of the rhizophore consists of large spherical parenchymatous cells containing starch and proteid granules. These cells are cut off externally by the cambium, which completely surrounds all three lobes of the rhizophore-stele apart from the region of the apical meristem (Pl. 40. fig. 80, and text-figs. 4, 5). The lobing of the caudex depends entirely upon the distribution of the cambium, since the three main furrows always coincide with the three narrow zones of primary meristem, from which, as stated above, relatively very few cortical cells are differentiated. This accounts for the almost spherical outline of the caudex of the very young sporophyte, in which the formation of secondary cortical tissue has not had time to proceed very far.

Owing to the centripetal development of the secondary cortical tissues, the diameter of the caudex rapidly increases ; but nevertheless a very considerable increase in height as compared with the increase in diameter is noticeable in old specimens (Pl. 33. figs. 4, 7). This result is brought about by the constant decortication of the older (*i. e.* most peripheral) region of the caudex. This process of decortication takes place in the following manner. Certain irregular patches of cortical cells situated at or near the periphery of the caudex are stretched by the mechanical pull exerted by the rapidly increasing radial growth of the secondary cortex (text-fig. 6). The walls of the cells bordering on these 'islands' or 'bays' of stretched parenchyma gradually become

suberized (text-fig. 7). These cells ultimately become torn apart, and in this way irregular fissures are produced in the oldest parts of the cortex (Pl. 33. fig. 7; Pl. 38. figs. 56–58).

It frequently happens that these fissures meet in the interior of the cortex, in which case irregular fragments of cortical tissue, including portions of unmodified parenchyma,

Text-fig. 6.

Isoëtes japonica. Diagram showing early stage of decortication. The stretched cortical cells are indicated by the areas included by the dotted lines. From a transverse section of a lobe of the caudex. × 6.

Text-fig. 7.

Isoëtes japonica. Diagram showing later stage of decortication. The dotted areas denote cells with suberized walls. From a transverse section of a lobe of the caudex. × 6.

Text-fig. 8.

Isoëtes japonica. Diagram showing a late stage of decortication. The fragment A is completely cut off from the cortex. From a transverse section of a lobe of the caudex. × 6.

become more or less isolated and finally break away (text-figs. 7, 8). The suberized cells bordering these fissures form a thin layer of periderm, which is continuous with that of the primary cortex of the stem and of the rhizophore. A somewhat similar

process takes place at the base of each of the three main furrows of the caudex. In these regions the primary cortical cells are greatly stretched in a plane at right angles to that of the furrow, whilst a few cells bordering on the stretched cells become feebly meristematic, dividing by periclinal walls (Pl. 33. figs. 1, 2). The walls of the stretched cells gradually become suberized and are finally torn apart (Pl. 33. fig. 3). In this way the main furrows increase in depth.

A series of transverse sections through the caudex of an old plant are represented in Pl. 38. figs. 55–59. The caudex immediately below the 'leaf-rosette' has a roughly circular outline, as shown in fig. 55. Immediately below this level the caudex begins to assume its trilobed form, but the grooves appear relatively shallow (fig. 56). Sections cut through the caudex at successively lower levels (figs. 57, 58, 59) show the typical tri-lobed outline, the three lobes of the caudex being very prominent in the rhizophore region of the caudex.

Development, Structure, and Arrangement of the Roots.

1. *Development of the Roots.*

We were unfortunately unable to investigate the development of the primary root, which was fully developed in the youngest plant we examined. The young roots, which are differentiated from the primary meristem of the rhizophore, penetrate the cortical tissues of the rhizophore and ultimately emerge from its lower surface. In *Isoëtes japonica* the root never undergoes dichotomy whilst the apex is still embedded in the cortex.

Our observations on the mode of growth at the apex of the root, so far as they go, confirm the account given by Farmer (14, pp. 51, 52). Distinct histogenetic layers are clearly shown, and the plerome appears to grow from a single initial cell. We also agree with this author that the root in the genus *Isoëtes* is really an early type of adventitious root.

2. *Structure of the Adult Root.*

The adult roots of *Isoëtes japonica* are essentially similar to those of other species of the genus. They are long and fibrous, and dichotomize repeatedly at a short distance from the caudex (Pl. 40. fig. 73). They have a dirty-brown colour, which is due to the suberization of their peripheral cells. In a young root, only the outermost layer of cells is suberized; but in older roots several layers of cortical cells may become suberized.

The roots bear numerous long unicellular root-hairs, which are most abundant towards the root-apex.

The general structure of the monarch vascular bundle of the root of *Isoëtes* is well known. It is surrounded by a well-defined endodermis, and occupies an excentric position in the root. The protoxylem, as a rule, is endarch; but a certain amount of irregularity in the position of the first-formed elements of the xylem was observed. The xylem consists of narrow tracheids with spiral or annular thickenings. True sieve-tubes

occur in the phloem (Pl. 35. fig. 17); they are in direct organic connection with the sieve-tubes of the rhizophore-stele.

3. *Arrangement of the Roots.*

The arrangement of the roots in *Isoëtes* has already been described by Von Mohl (24, p. 183), Hofmeister (16, p. 358), Scott and Hill (28, pp. 428–430), Stokey (32, p. 315), and Lang (20, p. 784).

However, a reinvestigation of this question, which was greatly facilitated by the large dimensions of *I. japonica*, has led us to put forward an entirely new interpretation.

The corm-like caudex of *Isoëtes* is perennial, and may live for very many years. The annual increment in the number of roots is very large indeed; Hofmeister (16 p. 359) states that as many as six generations of roots may be produced during the vegetative period of one year. Moreover, the duration of each root is far less strictly limited to any definite period than that of the leaves, which persist for one season only. Thus it

Text-fig. 9.

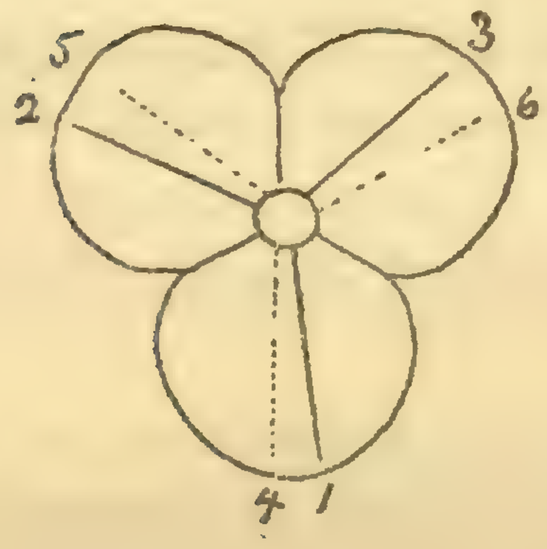
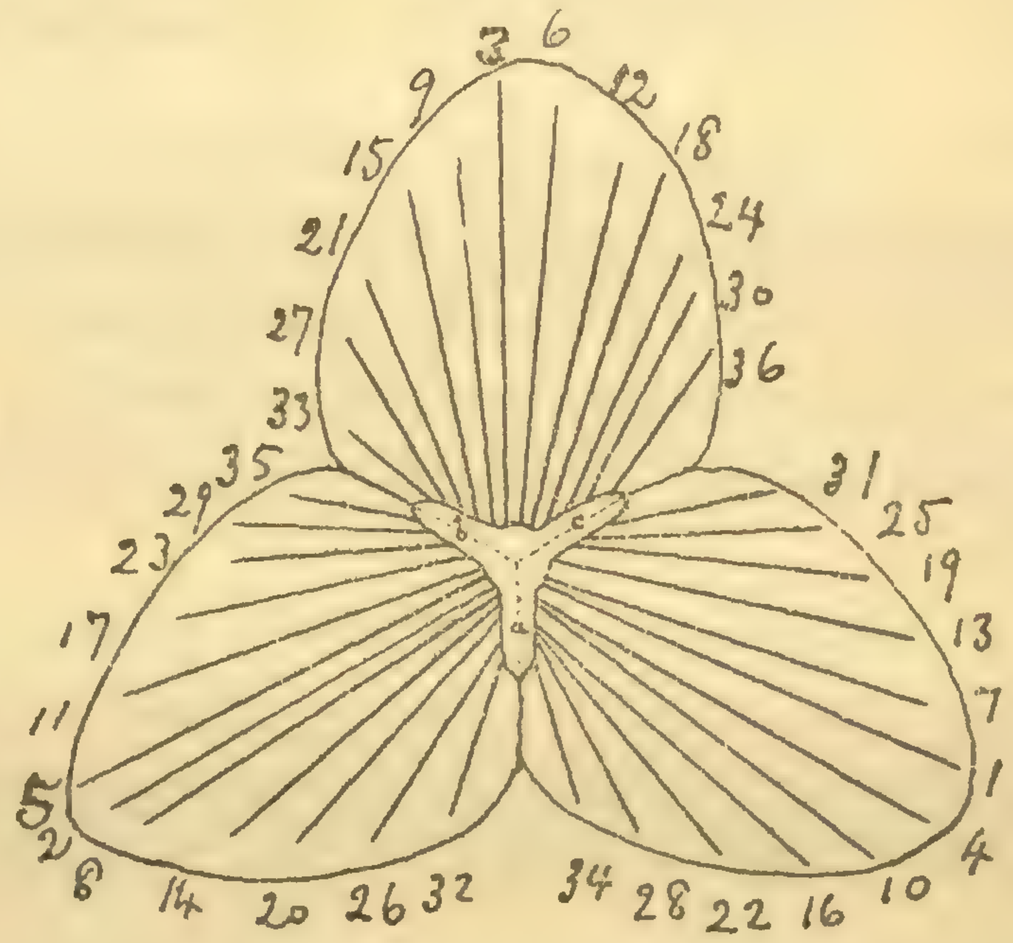


Diagram showing arrangement of the first six roots of a young plant of *Isoëtes japonica*. The roots are numbered consecutively.

Text-fig. 10.



Diagrammatic transverse section of the caudex of *Isoëtes japonica*, showing the order in which the roots are differentiated. Compare text-fig. 11.

follows that a very considerable area is required for the attachment of these numerous roots.

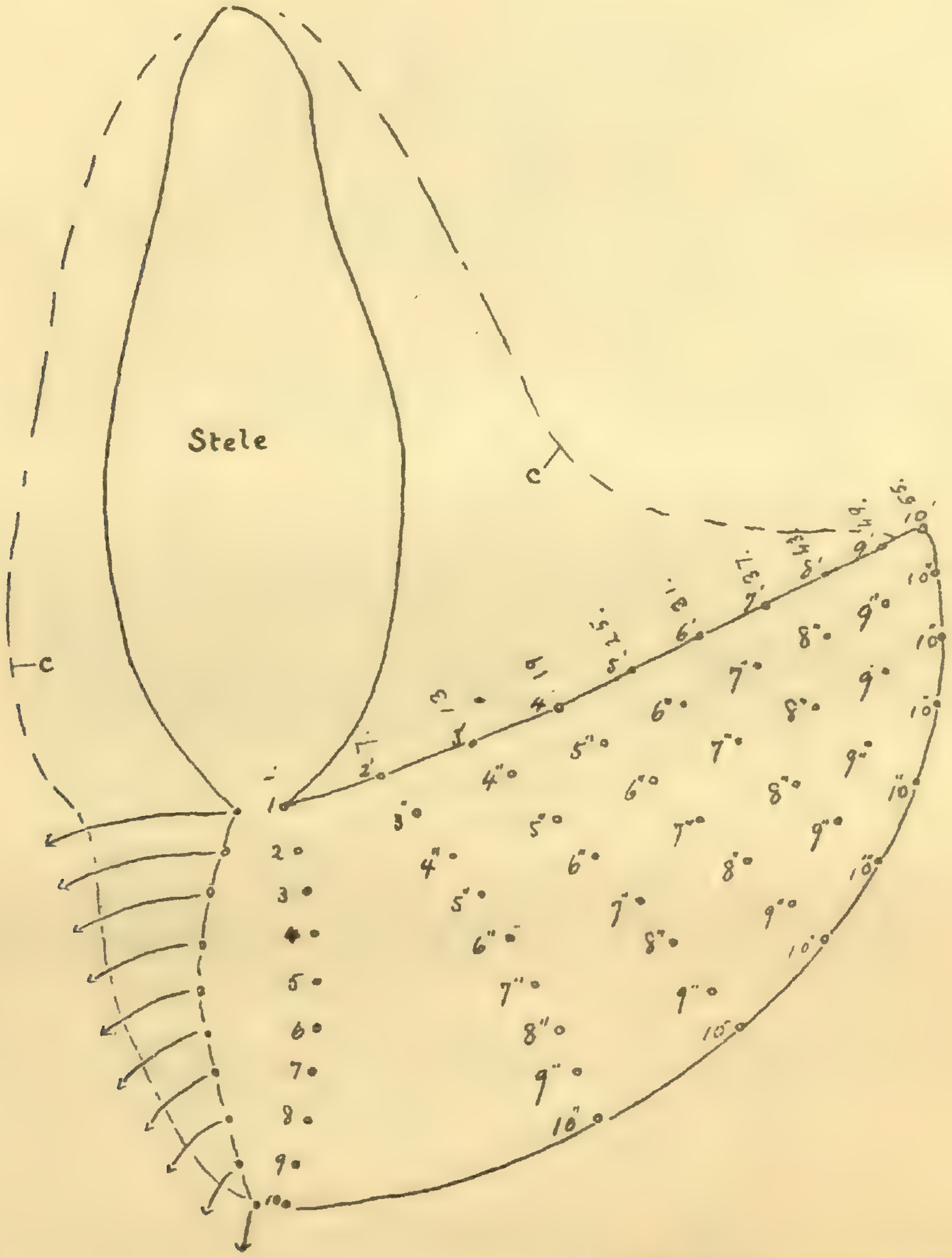
The roots are borne upon a specialized structure, the rhizophore, which in this genus must be regarded as an organ *sui generis*.

In the very young sporophyte, the first three roots, when fully developed, lie along the centre line of the three lobes of the caudex repectively (text-fig. 9). It must, however, be remembered that the caudex of the very young plant is roughly cylindrical; the lobing of the caudex shown in the diagram does not represent the actual state of affairs. The fourth, fifth, and sixth roots lie alongside the first, second, and third respectively (text-fig. 9). Even in the very young sporophyte, the primary meristem of the rhizophore can easily be distinguished at the base of the group of

tracheids produced at the junction of the first few root-traces (Pl. 40. fig. 75). From this primary meristem the young roots and the primary xylem, phloem, and cortex of the rhizophore are differentiated.

Differentiation of the primary tissues proceeds along three radiating, but slightly ascending, lines, which correspond to the three main furrows of the caudex as explained above (p. 346 *et seq.*). In this way, the stele of the rhizophore becomes

Text-fig. 11.



Isoëtes japonica. Diagram showing arrangement of roots on one flank of a lobe of the rhizophore-stele. *c* = cambium. (For explanation see text.) The consecutive numbers denote the succession of roots on one flank of a stelar lobe, whereas the numbers 1, 7, 13, 19, etc., denote the succession of roots on the plant. Compare text-fig. 10.

distinctly three-lobed, each lobe appearing irregularly triangular in a radial longitudinal section of the caudex cut in the plane of the corresponding main furrow.

The young roots are differentiated from the primary meristem of the rhizophore in rows (hereafter referred to as 'series') roughly parallel to the lower edge of the stelar lobe; these series rise in acropetal succession (text-fig. 11). All the roots belonging to

a series are differentiated simultaneously, that is to say, the roots belonging to a series are always of the same age. These series of roots are regularly arranged on both flanks of the stelar arms (text-figs. 4, 5).

Let us consider the roots which emerge from any one lobe of the caudex. Text-fig. 12 represents a drawing of the lower surface of one complete lobe of a fairly young plant of *I. japonica*, from which the roots had been artificially removed. It will be noticed

Text-fig. 12.

Part of the caudex of a young plant of *Isoëtes japonica* (*cf.* Pl. **33.** figs. 5 & 6) seen from below. **The roots have been artificially removed.**

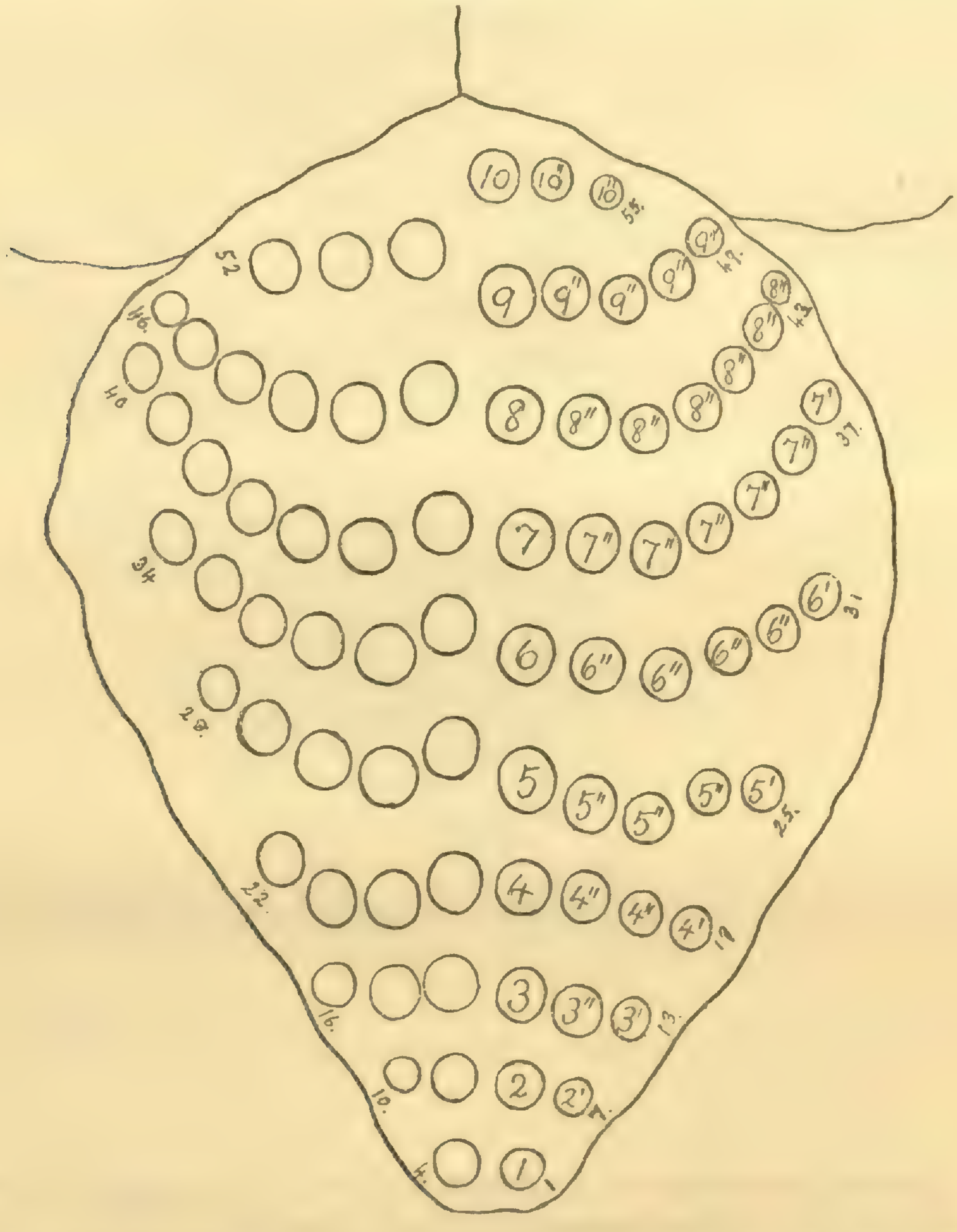
that the roots, as they emerge from the cortex, are arranged in several pairs of more or less curved series on the right and left halves of the lobe. This arrangement is to be explained by the fact that the series of roots which emerge from the right half of the lobe are derived from the flank of one arm of the rhizophore-stele, whereas those which

emerge from the left half of the lobe are derived from the flank of another arm of the rhizophore-stele (text-fig. 10).

In text-fig. 13, which was prepared from the same specimen, the roots which cannot be seen in a surface view of the actual specimen owing to the pronounced curvature of the edge of the lobe, are also included (*cf.* Pl. 33. fig. 6; Pl. 34. fig. 9).

In the diagram represented in text-fig. 11, the series of roots bear numbers corresponding to those of text-fig. 13; hence the oldest series, which always consists of a

Text-fig. 13.



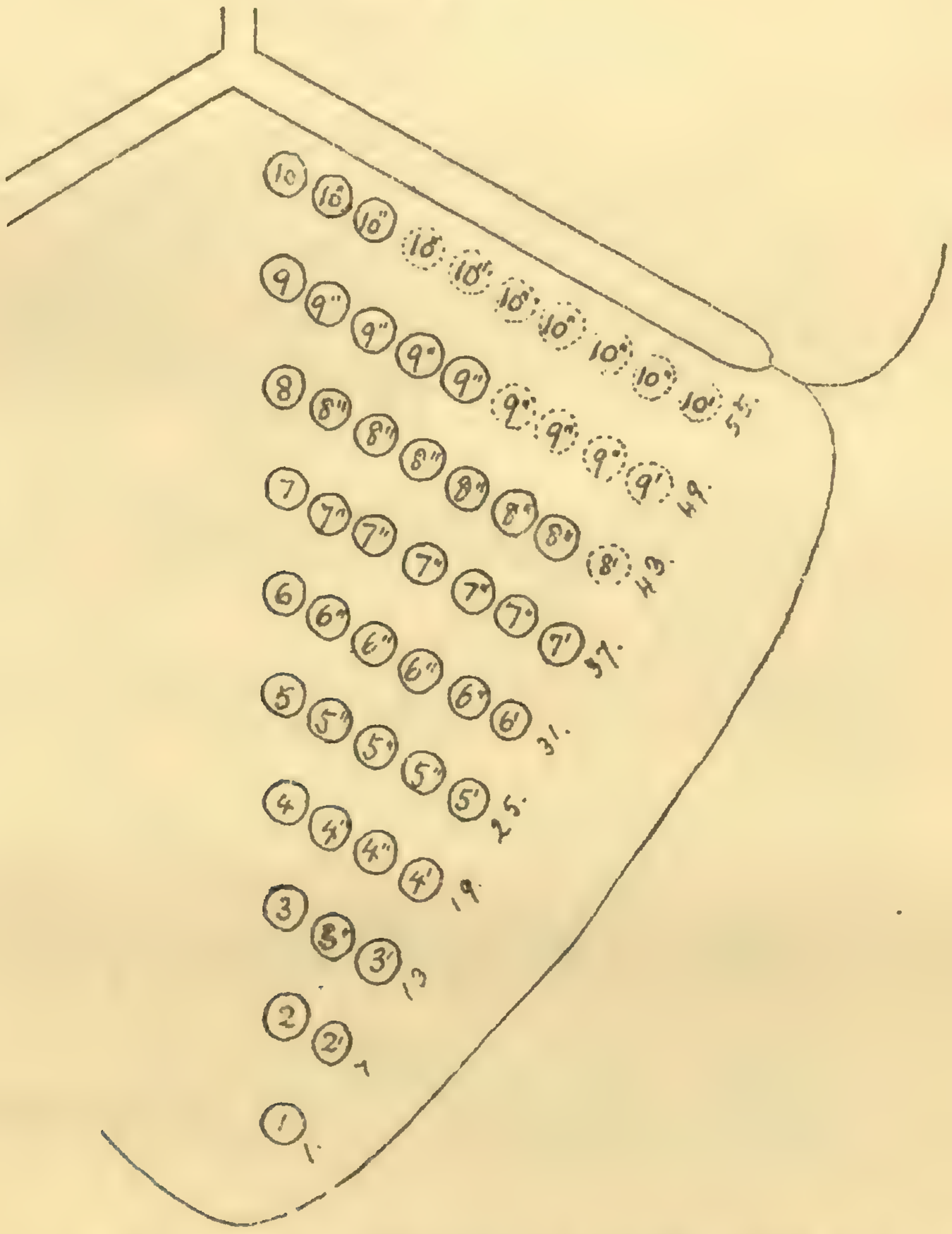
Isoëtes japonica. Diagram showing the actual arrangement of the roots on one lobe of the caudex represented in text-fig. 12. The roots are numbered as in text-fig. 11.

single root, is number 1. This root occurs on the extreme edge of the lobe, and in old specimens is invariably missing, since it is cut off together with the most peripheral portion of the lobe as soon as decortication takes place.

The theoretical arrangement of the roots, based upon the same specimen, is represented in text-fig. 14, in which all the roots of every series are shown. In this diagram every root differentiated by the primary meristem is made to appear on the surface of the caudex, whereas in text-fig. 13 only those roots which at that stage have actually appeared on the surface are represented. It so happens that the nearer the long axis of

the lobe a root is differentiated, the narrower the zone of cortical parenchyma it has to traverse before reaching the surface; it follows, therefore, that in any given series, all the roots of which are differentiated simultaneously, that root which has to travel the shortest distance before reaching the surface, *e. g.*, root 9 of series 9, represented in text-fig. 13, will be the first of that series to emerge from the cortex. As a result of the regular succession in the appearance of the roots of any series at the surface of the lobe, together with the more rapid centripetal production of secondary cortical cells in the centre of the lobe, the roots in this region are carried towards the outer margin of

Text-fig. 14.



Isoëtes japonica. Diagram showing theoretical arrangement of the roots on one half of a lobe of the caudex. The roots are numbered as in text-fig. 11.

the lobe (text-figs. 12, 13), the remaining roots of each series emerging at a point nearer the angle of the furrow.

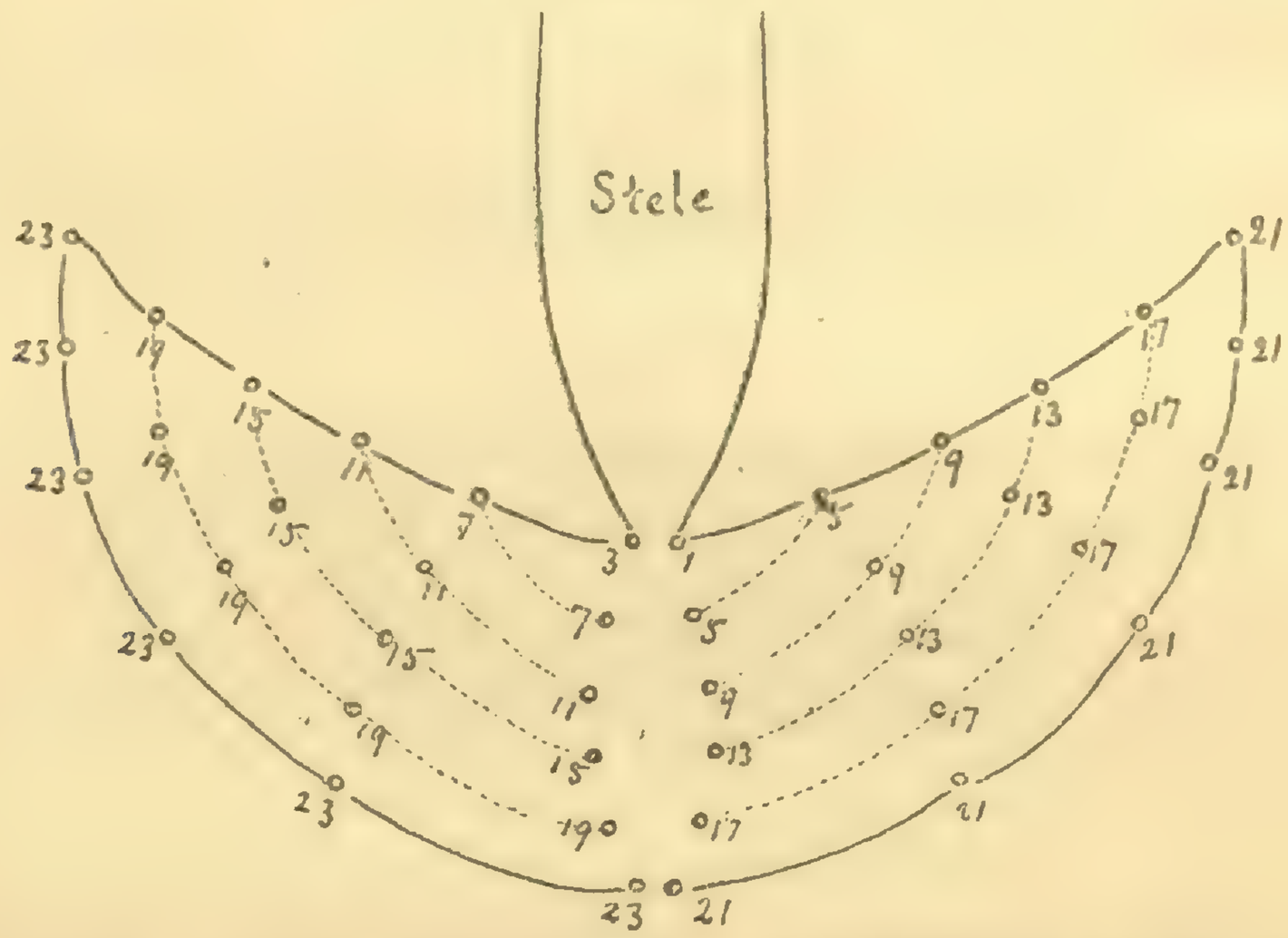
In this connection a brief description of the root-arrangement of those species, such as *I. lacustris*, *I. echinospora*, etc., which generally possess a bi-lobed caudex, may not be out of place. It is well known that the basal portion of the stele (*i.e.*, rhizophore-stele) of these bilobed forms has two arms which lie in the plane of the two main furrows of the caudex. In a median longitudinal section of the caudex cut parallel with the furrows, the rhizophore-stele appears crescent-shaped (text-figs. 2, 15; also *cf.* Von Mohl, 24, p. 183, Taf. 3. figs. 4, 9).

Roots from the two arms of the rhizophore-stele are arranged on the right and left halves of each lobe of the caudex respectively (text-figs. 15, 17).

In general, the arrangement of the roots on the flanks of the two stelar arms is essentially the same as in the tri-lobed species (compare text-figs. 15, 16, 17 with text-figs. 9, 10, 11; also *cf.* Stokey, 32, Pl. 19. fig. 6 *); further description is therefore unnecessary.

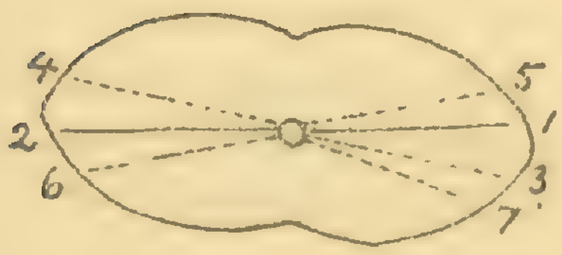
Before leaving the subject of the root-arrangement in *Isoëtes*, a very simple method of calculating the approximate total number of roots produced by any given plant may be mentioned. In text-figs. 11, 14, 15, 18, it will be noticed that the number of roots produced in any series always corresponds to the number of that series, *e. g.*, in series 1 there is one root, in series 2 there are two roots, in series 3 three roots, and so forth.

Text-fig. 15.



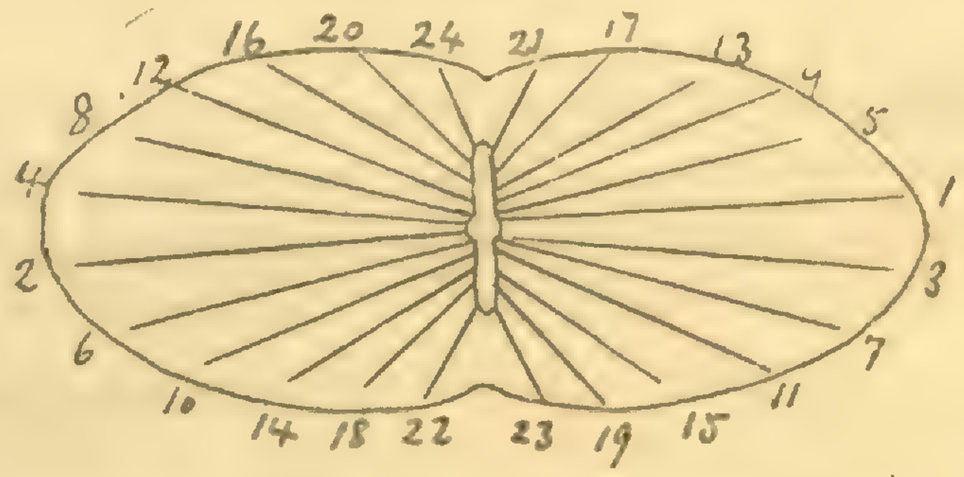
Isoëtes lacustris. Diagram showing arrangement of the roots on one half of the rhizophore-stele. The numbers correspond with those of text-figs. 16 and 17.

Text-fig. 16.



Isoëtes lacustris. Diagram showing the arrangement of the first seven roots of a young plant.

Text-fig. 17.



Isoëtes lacustris. Diagram showing order in which the roots are differentiated. From a transverse section of the caudex.

* Stokey (*l. c.* p. 315), however, states that "the youngest sets of roots are those nearest the furrow; and of those in the furrow the youngest are at the ends." This statement is incorrect, because all the roots belonging to any series are of the same age (see text-fig. 18).

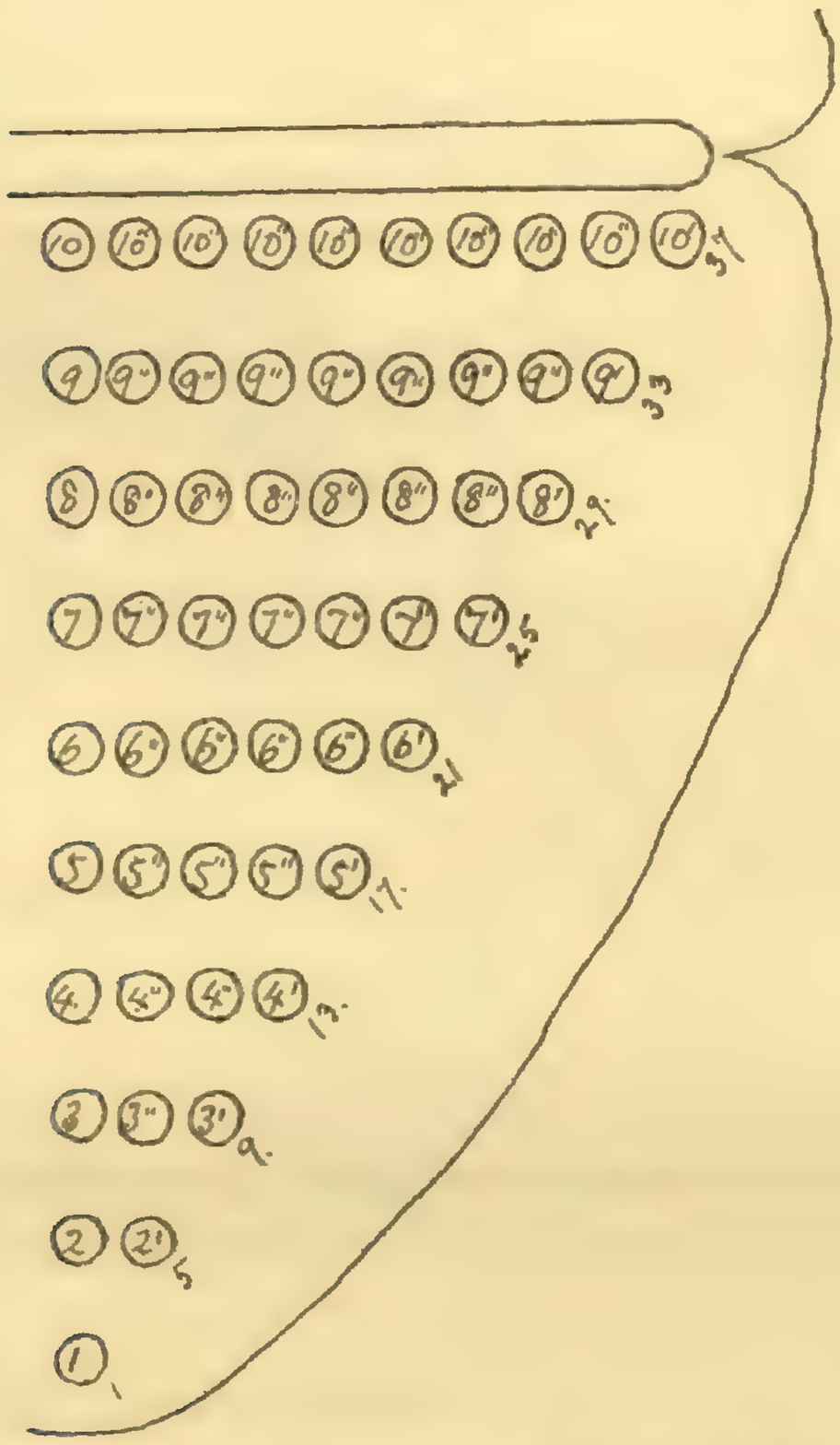
Therefore, if the number of series on a flank of either of the stelar lobes be determined *, then the approximate total number of roots produced by that plant may be calculated from the following formula, where

x = approximate total number of roots produced by the plant,
y = number of stelar lobes †,
z = number of series on the flank of a stelar lobe.

$$x = 2y\,\frac{z\,(z+1)}{2}$$

$$\therefore\ x = y\,z\,(z+1).$$

Text-fig. 18.



Isoëtes lacustris. Diagram showing theoretical arrangement of the roots on one half of a lobe of the caudex. The consecutive numbers denote the succession of roots on one flank of a stelar lobe, whereas the numbers 1, 5, 9, 13, etc., which correspond to those of text-figs. 15, 16, and 17, denote the succession of roots on the plant.

Arrangement of the Leaves.

As stated above, many leaves are produced every year. A. Braun (3, p. 34), referring to *Isoëtes setacea*, another tri-lobed species, says that even in a young specimen the leaves are arranged on the caudex in a spiral of complicated phyllotaxis. In young plants of

* The number of series can easily be determined from thick tangential hand-sections of the caudex cut parallel with the plane of a main furrow.

† Two in bi-lobed species and three in tri-lobed species, since the number of stelar arms is always equal to the number of lobes of the caudex.

I. japonica the phyllotaxis is $\frac{5}{13}$; but we were unable to determine the complicated phyllotaxis of older plants with any degree of accuracy. On the other hand, Hofmeister (16, p. 536) points out that the leaves of young plants of *I. lacustris*, a bi-lobed species, are always at first arranged in a distichous manner, the distichous arrangement gradually passing over into a spiral of increasing complexity, viz., $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, until finally an $\frac{8}{21}$ phyllotaxis is attained.

Development of the Leaves.

The primordia of the leaves arise from certain superficial cells of the primary cortex situated around the base of the apical protuberance (Pl. **39**. figs. 65–70). As a result of the luxuriant growth of these superficial cells of the primary cortical tissue, the primordia can very soon be identified as smaller or larger, flattened, more or less ovate, or crescent-shaped papillæ. Subsequent growth of the leaf, as Farmer (14, p. 46) has already described, is intercalary, the meristematic tissue being for the most part restricted to a zone (of varying thickness) at or near the base of the young leaf. Ultimately, however, this meristematic zone becomes localized in a region immediately above the insertion of the ligule.

It must be remembered, however, that considerable elongation results from the further growth, both in length and in diameter, of the individual cells of the leaf (*cf.* Wilson-Smith, 30, pp. 229–230).

That part of the procambial strand of the foliar bundle which traverses the primary cortex, is differentiated at a very early stage in the development of the leaf. It originates by the division of certain cells of the primary cortex, which retain their meristematic character for a considerable period. A strand of small cells, easily distinguishable by their relatively large nuclei, is produced in an upward and outward direction (Pl. **39**. fig. 70). The upper extremity of the strand extends to the base of the young leaf. Connection with the primary xylem and phloem tissues of the stem-stele is established by the downward prolongation of the procambial strand, the tissues of which are differentiated from the 'parenchymatous mantle.'

The differentiation of the procambial strand of the leaf immediately precedes the differentiation of the cambium of the stem from the outermost cells of the 'parenchymatous mantle'; hence it is evident that the developing leaf-trace is not interrupted either by the cambium itself or by the products of its activity. We agree with Farmer (14, p. 40) that Hegelmaier's statement that the cells of the cambium contribute to the formation of the leaf-trace is incorrect, for, as Farmer (*l. c.*) remarks, the particular direction of the division of the cells which take part in the formation of the leaf-trace is determined *before* the cells in their vicinity assume the freshly active meristematic condition.

Further differentiation of the procambial strand of the leaf takes place centrifugally, the cells of the basal part of the strand being the first to become converted into tracheids, sieve-tubes, etc. This process gradually extends upwards and outwards towards the base of the leaf until finally the lamina is reached.

Anatomy and Histology of the Leaves.

1. *Epidermis.*

The epidermis of the leaf of *Isoëtes japonica* exhibits no special features, although the outer wall is very highly differentiated for a water-plant. The outer wall is comparatively thick (4–8 μ), and consists of an inner cellulose layer and an outer cuticularized layer (Pl. **36**. figs. 22, 23). The outer surface of the epidermis is covered by a very thin layer of cuticle. The primary membrane of the epidermal cells is very conspicuous, particularly in the parting-wall between adjacent cells. On the inner side of the primary membrane the cell-wall consists chiefly of cellulose, but on the outer side the thickening is more or less cuticularized. This well-marked differentiation of the outer cell-wall into two distinct layers appears to have a mechanical, but not a physiological, function. Moreover, this type of epidermis is not peculiar to *Isoëtes* amongst water-plants; it also occurs, for instance, in the stem of *Ranunculus fluitans*. A comparison of Pl. **36**. fig. 23 with Pl. **36**. fig. 22 will show that the outer wall of the epidermis is somewhat thicker in the lamina than in the basal region of the leaf. The cells of the epidermis usually contain chlorophyll granules.

2. *Stomata.*

The apical portion of the leaf, unless it be completely submerged, is usually provided with stomata. These stomata are of the gramineous type (Pl. **36**. figs. 23, 24), and possess no subsidiary cells. It appears, therefore, that a stoma-mother-cell divides but once longitudinally and forms a stoma directly. The guard-cells are provided with a conspicuous outer ridge.

3. *Mesophyll.*

Large air-canals, which are always four in number, traverse the mesophyll. The development of these lacunæ, which are formed by the lysigenous degeneration of certain definite groups of cells in the very young leaf, has already been described in detail by Farmer (14, p. 47) and by Wilson Smith (30, p. 230 *et seq.*). In these lacunæ, transverse septa or diaphragms occur at intervals of a few millimetres. The individual cells of these diaphragms have the stellate form commonly found in such structures, especially amongst water-plants (Pl. **36**. fig. 28).

No distinct palisade tissue is formed, most of the mesophyll cells containing abundant chlorophyll (Pl. **36**. figs. 23, 41). The cells bordering the lacunæ towards the centre of the leaf are always empty; that portion of their wall which abuts on the lacuna is slightly cuticularized (Pl. **36**. fig. 41).

Towards the base of the leaf the mesophyll cells contain very little chlorophyll, but occasionally the presence of reserve starch can be detected in these cells.

Whereas in some specimens of *I. japonica* the leaves possess hypodermal groups of fibrous elements, in others no trace of these tissues can be detected. The presence or absence of the hypodermal fibrous strands probably depends entirely upon the environmental conditions to which the leaves are subjected at a very early stage in their

development. A somewhat similar conclusion was arrived at by Yapp (36) as a result of his ecological studies on several morphological features exhibited by *Spiræa Ulmaria*. These strands are differentiated from the mesophyll parenchyma, and normally form four main and two accessory groups of fibre-like cells. Of the former, three are situated on the adaxial and only one on the abaxial side of the leaf. The accessory strands occur between the dorsal and corner strands. The main strands are very well developed, but, even in the terrestrial species (e. g. *I. Hystrix*), the individual fibres are only slightly lignified. Possibly these strands have but little mechanical significance; lignification of a cell-wall, whilst increasing the rigidity of the cell, decreases its strength. It was found, even on the same plant, that some leaves possessed these strands whilst others did not, and it sometimes happens that only three or four strands are developed. Moreover, individual strands do not necessarily extend along the whole length of the leaf, but usually show a tendency to die away or even completely disappear at certain points, especially in the basal region of the leaf. This fact may be correlated with the intercalary growth of the leaf, since the region of meristematic activity is situated near the base of the leaf.

Towards the margin of the leaf, particularly near the base, the cells become tangentially elongated, and their walls are thickened but not lignified.

4. *Vascular Bundle.*

A single collateral vascular bundle with normal orientation occupies an approximately central position in the leaf. The vascular bundle in the adult leaf is surrounded by a layer of large cells, which are fairly compact and regularly arranged. This row of cells probably constitutes the true endodermis, for although the radial walls of these cells are unthickened, yet they are highly refractive and present a more or less wavy appearance.

Immediately within this layer of cells we find a varying amount of conjunctive parenchyma, amongst which a few schizogenous canals are formed. These canals (= caneaux aérifères of Janczewski, 17) arise at a very early stage in the development of the leaf, *i. e.*, before the differentiation of metaxylem and metaphloem. The walls of the cells bordering these canals are not cuticularized.

For our present knowledge of the structure and development of the phloem tissues of the leaf of *Isoëtes* we owe much to the excellent work of Kruch (19), who made a comparative study of the conducting tissues of the leaves of several distinct species. Whereas the development of the xylem tissues varies in a striking manner in different parts of the leaf, the phloem tissues, on the other hand, are well developed throughout the whole length of the leaf.

In the young leaf, the phloem consists of sieve-tubes without companion-cells, and parenchyma. The former are arranged in an arc with its concave side facing the xylem. Protophloem occurs in the central part of the phloem-arc, whilst the later-formed sieve-tubes are usually collected together into two lateral groups separated from one another by the few protophloem elements, which, at a later stage, appear as a very narrow layer of crushed cells surrounded by ground-tissue. In the mature leaf,

the cells of the ground-tissue surrounding the protophloem undergo a considerable change. They appear to undergo considerable elongation, and their walls, although remaining cellulosic, become greatly thickened. These cells, according to Kruch, have a mechanical function. The thick-walled cell figured by Janczewski (17, Pl. 4. fig. 9) and designated a sieve-tube, evidently represents one of these modified conjunctive cells, which do not in the least resemble the sieve-tubes.

The sieve-tubes are composed of elongated cells with more or less inclined terminal walls (Pl. **37**. figs. 43, 44). Sieve-areas of the usual Cryptogamic type occur in abundance, both on the lateral and terminal walls of these cells. They are often rendered very conspicuous by a deposition of callus (Pl. **37.** figs. 43, 44).

Sieve-tubes of a similar nature are also found in the leaves of *Isoëtes lacustris* (Pl. **37.** fig. 45).

In both species the sieve-tubes of the foliar bundle connect up directly with similar elements of the primary and of the secondary phloem of the stem-stele (Pl. **34.** fig. 13; Pl. **35**. figs. **15, 21**).

The xylem of the foliar bundle consists of tracheids and parenchyma. Towards the apex of the leaf the tracheids are very feebly developed, only a few metaxylem elements being present besides the canal formed by the disorganization of a single protoxylem element. Here the position of the protoxylem is exarch (Pl. **37**. fig. 46). The transverse or slightly oblique terminal walls of the protoxylem elements are reticulately thickened, the thickening being lignified (Pl. **37**. figs. 49, 50). The primary membrane does not break down; hence the protoxylem canal consists of several superposed tracheids, with almost horizontal terminal walls, and is not a *trachea* in the strict sense, since only the annular thickenings of the lateral walls become disorganized. These protoxylem canals are said to conduct water; they must, therefore, retain their original function even after the disorganization of the secondary thickening.

In the adult leaf the protoxylem canal is always surrounded by a layer of regularly arranged cells, the morphological nature of which has never been satisfactorily explained. In *I. japonica* the radial walls of these regularly arranged cells, as well as that part of the wall which abuts on the canal, are slightly thickened, highly refractive, do not dissolve in strong sulphuric acid, and present most of the characters usually associated with an endodermis. Scott and Hill (28), and Janczewski (17), have regarded this row of cells as a true endodermis, but we prefer to apply the term 'pseudo-endodermis' to these cells, since they differ from a typical endodermis both in origin and position. In the lower region of the young leaf it is evident that the protoxylem elements are surrounded by a distinct row of cells, some of which are typical metaxylem tracheids, whilst others are parenchymatous (Pl. **37**. fig. **47**). Thus, in this part of the leaf some of the 'pseudo-endodermal' cells are homologous with the water-conducting elements of the foliar bundle. The fact that these cells occur in the centre of a vascular bundle and generally surround only one of many tracheids, is sufficient evidence to show that they do not constitute a true endodermis. Moreover, the slight thickening and cuticularization of the radial walls of these cells are not features that occur only in endodermal cells: a layer of cells exhibiting all the characters generally associated with an endodermis

completely surrounds the glossopodium of the ligule (Pl. 36. fig. 42). In *Elodea*, and in some species of *Potamogeton*, the lysigenous protoxylem canal is surrounded by a row of regularly arranged cells, the radial walls of which, however, do not appear to be cuticularized.

As many as five protoxylem canals may be found in the supra-ligular region of the leaf. They are invariably formed by the disorganization of protoxylem elements, and are always surrounded by a row of 'pseudo-endodermal' cells.

In the ligular region of the leaf a marked increase in the number of metaxylem elements is found, but the position of the protoxylem remains exarch (Pl. 37. fig. 48). In the sporangial region of the leaf, and lower down also, a few metaxylem elements are differentiated on the phloem side of the protoxylem, while many are present on the opposite side; hence, in this region of the leaf, the protoxylem is mesarch.

The metaxylem of the laminar portion consists of elongated spiral or subreticulate tracheids with very oblique terminal walls (Pl. 37. fig. 51). In the sporangial region the tracheids are somewhat wider, have less oblique terminal walls, and pursue a sinuous course. In that part of the leaf-trace which traverses the cortex of the stem the xylem is better developed and more compact than in the leaf itself. Sooner or later, however, the conducting tissues become more or less stretched as a result of the formation of fresh secondary tissues (*i. e.*, phloem and cortex) by the cambium, and of the increase in size of individual cells of the cortex of the stem. For this reason the tracheidal elements of an old leaf-trace embedded in the cortex become greatly distorted. On the other hand, the xylem parenchyma, which retains its meristematic condition for a considerable period, is able to adapt itself to the changing proportions of the surrounding cortical tissue by dividing both transversely and longitudinally (Pl. 37. fig. 54).

The phloem is subjected to a similar strain, but its complete destruction is somewhat delayed by repeated divisions of the phloem-parenchyma. As a result of this cell-division the leaf-trace traversing the cortex becomes much wider with age (Pl. 37. fig. 54).

5. *Ligule.*

The earlier stages in the development of the ligule of *I japonica* agree with those described and figured for *I. echinospora* and *I. Engelmanni* by Wilson Smith (30, p. 232, Pl. 14. figs. 12–19). The ligule arises from a single epidermal cell of the very young leaf (Pl. 36. fig. 35). This cell contains very dense protoplasm, and rapidly increases in size; it then divides by a periclinal wall into two daughter-cells (Pl. 36. fig. 36), each of which immediately divides again by periclinal walls (Pl. 36. fig. 37).

The apical region of the young ligule divides most vigorously, and ultimately gives rise to the laminar portion, whilst, by the subsequent growth of the basal region, the glossopodium and ligular sheath are formed (Pl. 36. figs. 38–40; also *cf.* Pl. 39. figs. 66, 68).

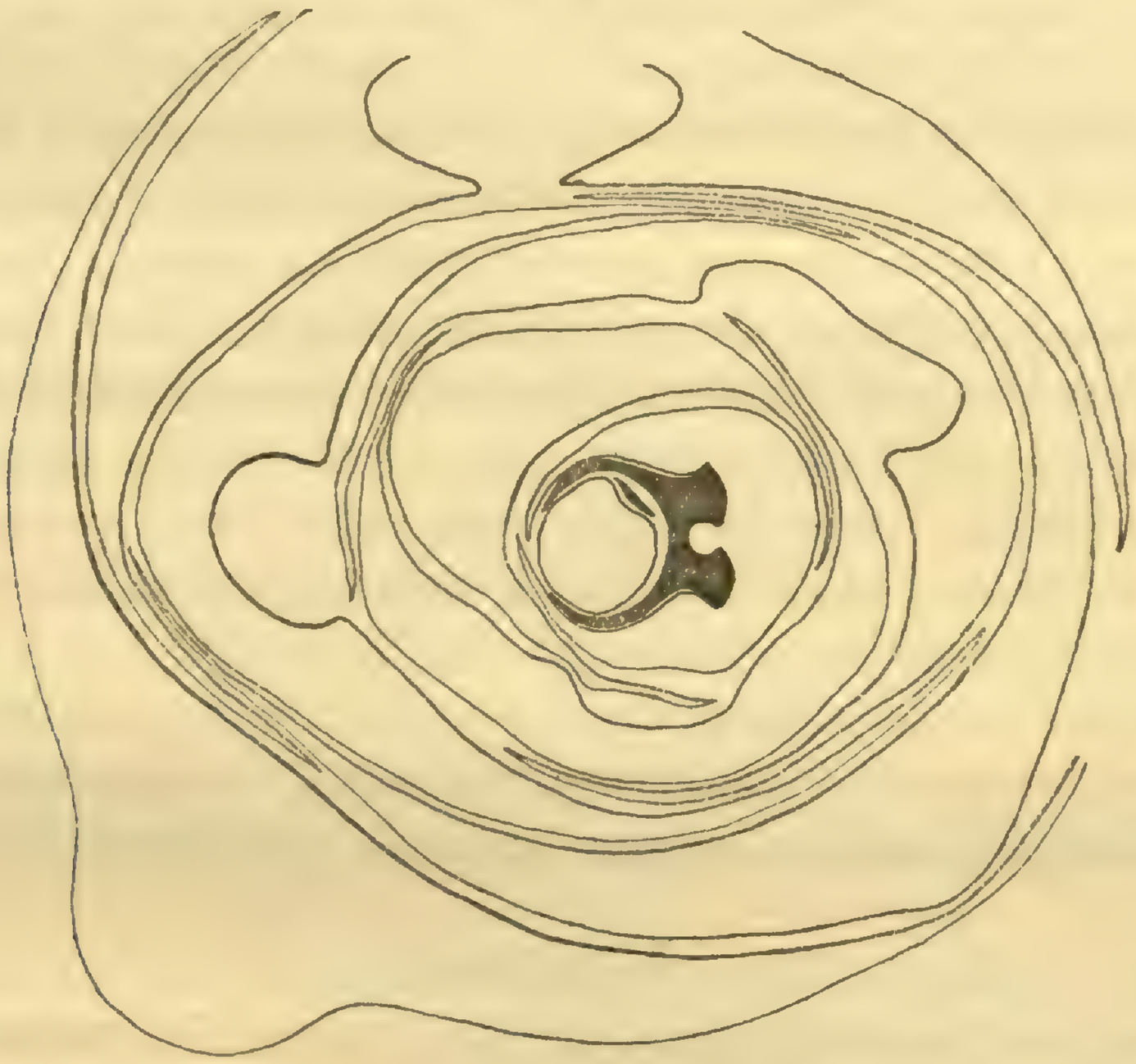
The form of the mature ligule is ovate-lanceolate, cordate at the base, with a lacerate margin (Pl. 36. figs. 25–27, 33). The central region of the ligule is many cells in thickness, but towards the margin it is never more than one cell in thickness. The laceration of the margin is brought about by a very peculiar method of sliding growth.

The individual cells of the marginal region exhibit unequal growth, as a result of which they become very loosely attached to one another, and ultimately produce narrow, irregular lobes (Pl. **36**. fig. 34).

The cells of the thicker central region of the ligule form a very loose tissue, and enclose large intercellular spaces (Pl. **36**. figs. 30–32). Even the epidermal cells are not compact; they are always covered with a very thin, but nevertheless quite distinct cuticle, which does not follow the outline of the cells, but leaves small intercellular spaces between them, thereby producing an effect which recalls that produced in the leaves of a plum-tree when attacked by the 'silver-leaf' fungus (=*Stereum purpureum*).

The cells of the lamina of the ligule have dense protoplasmic contents; these cells secrete mucilage (Pl. **36**. figs. 29–31). The secretion of mucilage by the ligule has

Text-fig. 19.



Isoëtes lacustris. Transverse section through base of leaf-rosette. The ligules are darkly shaded. × 20.

previously been described for *I. lacustris* by Farmer (14, p. 44), and for *I. Hystrix* by Scott and Hill (28, p. 442).

The cells of the glossopodium are very large, and contain relatively little protoplasm; but in *I. japonica* a band of large empty cells, such as Wilson Smith describes and figures for *I. echinospora* (30, p. 233, Pl. 14, *g* in fig. 22), was never observed.

The glossopodium is surrounded by a sheath of more or less isodiametric cells, the central portion of the radial walls of which appears to be lignified (Pl. **36**. fig. 42). This structure, which closely resembles an endodermis, has already been described and figured by Bruchmann (7, p. 576, Taf. 24. figs. 22–25).

Certain cells of the leaf-base outside the glossopodium become converted into short reticulate tracheids. These elements, which are invariably found in close proximity to

the ligule, frequently abutting directly upon the ligular sheath, occur both in the fertile and in the sterile leaves. They are not continuous with the tracheids of the leaf-bundle, so that their function is probably not water-conduction but water-storage. However, since these cells are also present in *I. lacustris*, which is practically always submerged, it is possible that their original function has been lost.

Bud-Protection.

We have already mentioned that the apex of the stem together with the youngest leaves and leaf-rudiments are situated at the base of a comparatively deep depression in the cortex (Pl. **33**. figs. 7, 8). Thus they are surrounded on all sides by cortical tissue, whilst above they are completely enclosed within a canopy formed by the overlapping

Text-fig. 20.

Isoëtes japonica. Transverse section through leaf-rosette. The ligules are darkly shaded. × 10.
m = mucilage.

vaginæ of the older leaves. In some species, e. g. *I. lacustris*, the wings of the leaves are of sufficient width to completely enclose the next younger leaf (Pl. **37**. figs. 52, 53, and text-fig. 19). In this species the ligule is relatively very small. The wings of the leaves of *I. japonica*, on the other hand, are not sufficiently broad, except at the very base of the leaf. Their protective function, however, is taken over by the ligule, which is remarkably well developed in this species (text-fig. 20). The ligule not only envelops, and thus protects, the younger leaves, but provides an additional protective device in the form of a copious secretion of mucilage. This secretion of mucilage is particularly abundant in the youngest ligules, *i. e.* those found in the very centre of the leaf-rosette, and therefore it usually happens that the actual apex of the stem is covered with a film of mucilage (*m* in text-fig. 20).

Systematic Observations.

A. Braun (4), describing the present species for the first time, expressed the opinion (*l. c.* p. 460) that it belonged to his section "palustres s. amphibiæ" of the genus *Isoëtes*. In a later and more detailed account of this species the same author (5, p. 8) retained this classification *. Some years later, in 1882, Motelay and Vendryés (25, p. 318) placed this species in their section "palustres," which, together with the section "amphibiæ," they had established on the above-mentioned group of A. Braun. Baker (1, p. 132), on the other hand, transferred it to the group "Amphibiæ" †. Sadebeck (27), in a more recent work on *Isoëtes*, placed *I. japonica* in the section "amphibiæ," following A. Braun in his classification of the genus.

We are perhaps justified in taking advantage of this opportunity of discussing the classification of this genus.

A brief summary of the various classifications which have been put forward is given below in order of priority :—

1. Alex. Braun (5, p. 8; 6, p. 598), followed by Milde (23) and by Sadebeck (27).
   Section 1. Aquaticæ (s. Submersæ).
      Leaves with wide lacunæ, the outer wall of which, including the epidermis, consists of from 2–3 layers of cells; stomata, hypodermal fibres, phyllopodes, and phyllades ("Niederblätter") absent.
   Section 2. Amphibiæ (s. Palustres).
      Leaves as in 1; but with stomata and groups of hypodermal fibres, usually 6 in number. Phyllopodes and phyllades absent.
   Section 3. Terrestres.
      Leaves with narrow lacunæ, the outer wall of which consists of only one layer of cells, *i. e.* the epidermis itself; stomata numerous; 4 large groups of hypodermal fibres; phyllopodes and phyllades present.
2. Motelay and Vendryés (25, p. 317).
   Group 1. Aquaticæ.
   Section 1. Submersæ.
      Leaves with wide lacunæ, the outer wall of which consists of from 2–3 layers of cells. Phyllopodes and phyllades absent.
   Section 2. Palustres.
      Leaves as in 1; but 6 groups of hypodermal fibres present without exception. Phyllopodes absent. Phyllades absent, or, if present, very feebly developed.
   Section 3. Amphibiæ.
      Leaves as before, with 6 groups of hypodermal fibres; stomata usually present. Phyllopodes and phyllades absent.

* In an appendix to the paper, Braun refers to this section as "Palustres s. Inundatæ" (*l. c.* p. 33).

† Baker established a fourth group, "Subaquaticæ," characterized by the presence of stomata and the absence of hypodermal strands.

Group 2. Terrestres.

Leaves with narrow lacunæ, the outer wall of which consists of only one layer of cells. Stomata numerous.

Only 4 groups of hypodermal fibres present. Phyllopodes present, with or without spines; the phyllades forming a scale.

3. Baker (1, p. 124).

Group 1. Aquaticæ.

Plants permanently submerged. Leaves without stomata, groups of hypodermal fibres, or phyllopodes.

Group 2. Subaquaticæ.

Plants inhabiting shallow water. Leaves with few stomata, but without groups of hypodermal fibres. Phyllopodes absent.

Group 3. Amphibiæ.

Plants inhabiting shallow water, where they are subjected to desiccation during certain periods of the year. Leaves with groups of hypodermal fibres; stomata abundant. Membranous leaf-bases occasionally persistent.

Group 4. Terrestres.

Plants growing in damp or water-logged soil. Leaves with groups of hypodermal fibres; stomata abundant. Phyllopodes present.

4. Eaton (13, pp. 58, 59) *.

§ 1. Aquaticæ, A. Br.

Plants submerged; leaves cylindrical, fleshy, without groups of hypodermal fibres or stomata.

§ 2. Amphibiæ, A. Br.

Plants of inundated shores or tidal flats; leaves with stomata, but without groups of hypodermal fibres.

§ 3. Palustres, A. A. Eaton.

Plants inhabiting the extreme edge of ponds or streams; leaves with stomata and groups of hypodermal fibres.

§ 4. Terrestres, A. Br.

Plants inhabiting dry situations; leaves setaceous with numerous stomata and 4 groups of hypodermal fibres; velum absent.

Using the above classifications it would be very difficult to determine the section in which *I. japonica* should be included. For instance, this species may grow in situations where the plant is always completely submerged, or it may grow on damp soil at least for a short period. On the one hand, it produces leaves devoid of both stomata and hypodermal fibres; on the other hand, the leaves are provided with both fibres and stomata or with groups of fibres alone †. Thus one and the same species may belong to "Aquaticæ" of A. Braun and of Baker, to "Submersæ" of Motelay and Vendryés, to "Amphibiæ" of A. Braun and of Baker, and to "Palustres" of Motelay and Vendryés and of Eaton.

* Includes North-American species only.

† It is possible that specimens may be found with stomata but without groups of fibres.

Let us take another example. *Isoëtes echinospora* is always regarded as belonging to "Aquaticæ," auct., or to "Submersæ," Mot. et Vendr. Nevertheless, the var. *Braunii* would fall into the section "Subaquaticæ," Bak., and has actually been placed in the "Amphibiæ," Eaton (13, p. 58)*. It is surely absurd that a species and its variety should belong to different sections!

The following examples also demonstrate the weak points in these artificial classifications:—

I. saccharata, placed by Motelay and Vendryés in their section "Palustres," is transferred by Baker to his "Subaquaticæ."

I. tegulensis is also regarded by Motelay and Vendryés as belonging to section "Palustres"; Baker, however, considers it to be one of the "Amphibiæ."

I. Tuckermanii, according to Baker, belongs to the group "Subaquaticæ," but is placed in "Aquaticæ" by Eaton.

I. Butleri furnishes us with a more extreme case. This species is placed in "Amphibiæ" by Motelay and Vendryés and by Baker, whereas Eaton regards it as the sole representative in North America of the most distinct section "Terrestres." However, an examination of the specimens collected by B. F. Bush at Eagle Rock, Missouri, on May 22nd, 1898, has convinced us that this species cannot belong to "Terrestres," A. Br. In arriving at this conclusion we were influenced by the account given by Geo. D. Butler (9, p. 2), the discoverer of the plant. This species is closely related to *I. melanopoda*, a species belonging to "Amphibiæ," but prefers less humid situations. Presumably Eaton considered the last-mentioned character of sufficient importance to justify its inclusion in the section "Terrestres"! But according to its morphological and anatomical characters, this species should be placed in the section "Amphibiæ." The definition which Eaton (13, p. 59) gives for section "Terrestres" may fit *I. Butleri*, but does not agree with A. Braun's definition of "Terrestres."

All the above-mentioned discrepancies point to the fact that the existing classifications of the genus *Isoëtes* are both unnatural and arbitrary, being based for the most part on certain very unstable morphological characters, which have been shown to vary with the environmental conditions of the plant.

Isoëtes japonica furnishes us with a very clear case of this correlation of anatomical characters with the habitat relations of the plant, since it may acquire the characters of at least three different sections of the genus.

It is evident that species usually included in sections "Aquaticæ" or "Submersæ" may so alter their characters as a direct result of a change in their environment (*e. g.* by adopting an amphibious mode of life) as to justify their inclusion in "Subaquaticæ." In the same way, there can be but little doubt that any species of "Amphibiæ" may live entirely submerged or may even adopt a "terrestrial" habit. Possibly the species belonging to "Terrestres" are only extreme forms of "Amphibiæ." We are therefore led to the conclusion that this artificial division of the genus *Isoëtes* into sections can serve no useful purpose.

We may, however, distinguish two sections, comparable to the primary groups of

* Eaton regards A. Braun as the author of this section, but his definition does not correspond to that of "Amphibiæ," A. Br.

Motelay and Vendryés, viz. "Aquaticæ" and "Terrestres" (25, p. 317). But we are of the opinion that the use of these names is misleading and should therefore be avoided. The chief characters of the two sections are as follows :—

Section 1. Eu-Isoëtes, nob.

Leaves with 4 wide lacunæ, the outer wall of which is composed of 2–3–5 layers of cells (including the epidermis); sometimes provided with hypodermal fibrous strands, normally 6 in number, 4 main (1 abaxial and 3 adaxial) and 2 accessory (lateral). Sterile leaves very similar to the sporophylls. Leaf-bases seldom persist as membranous scales, never forming phyllopodes.

Species growing either submerged, in shallow water (where they are subject to temporary desiccation), or in damp soil.

Section 2. Cephaloceraton, Gennari (gen.).

Leaves with 4 narrow lacunæ, the outer wall of which consists of one layer of cells (*i. e.* the epidermis alone); normally provided with only 4 hypodermal fibrous strands (1 abaxial and 3 adaxial). Sterile leaves conspicuously smaller than the sporophylls, eventually giving rise to phyllopodium-like scales. Leaf-bases always form persistent phyllopodes.

Includes species inhabiting damp soil, subject to desiccation during a certain period of the year.

Discussion.

The systematic position of *Isoëtes* still remains undecided. This genus has in turn been compared with: 1. Certain Angiosperms (Hofmeister); 2. Eusporangiate Ferns (Vines, Farmer, and Campbell, 10); 3. Lycopods (including Lepidodendreæ, Sigillarieæ, and *Pleuromeia*) (Wilson Smith, Scott & Hill, Bower, Stokey, and Lang) *.

The supposed resemblance between *Isoëtes* and the Angiosperms is both fanciful and unscientific, and cannot be accepted as any indication of affinity.

The Filicinean affinities of this genus are almost entirely based upon gametophytic characters, the importance of which, however, is too frequently underestimated.

With regard to the morphology and anatomy of the sporophyte, *Isoëtes* has many characters in common with the Lycopodineæ (in the wider sense), but these are not of sufficient importance to justify the view that *Isoëtes* belongs to this group.

The isolated position of the genus *Isoëtes* amongst recent Vascular Cryptogams has also been suggested, a separate Class, the Isoëtales, co-ordinate with the Filicales, Lycopodiales, Sphenophyllales, etc., being proposed for its reception (Campbell, 10 A; followed by Lotsy, 21).

The evidence derived from the present anatomical investigation is distinctly favourable to this view.

In the structure of the stem-apex and the development of the primary tissues of the stem, *Isoëtes* differs in many respects from *Lycopodium* or *Selaginella*, while the

* In these papers the systematic position of *Isoëtes* is discussed in detail; recapitulation is therefore unnecessary.

secondary tissues of this genus bear no resemblance whatever to those of any species of *Lepidodendron* or *Sigillaria* hitherto examined.

The presence of a distinct root-bearing organ does not necessarily indicate any affinity with the recent or fossil Lycopods which possess such a structure (e. g. *Selaginella*, *Stigmaria*, *Pleuromeia*, etc.).

On the other hand, the anatomy of these structures is quite unlike that of the rhizophore of *Isoëtes*, to which even the four-lobed root-bearing basal region of the caudex of *Pleuromeia* bears only a superficial resemblance. Whereas in the latter the lobes of the stele are situated in the centre of the caudex lobes (31, Taf. 8. fig. 6), in the former they alternate with the lobes of the caudex and correspond in position to the main furrows.

It is not unlikely that a distinct root-bearing organ has been developed along two or three lines of descent, in which case the possession of a rhizophore is of little or no value in determining the phylogenetic position of a plant.

Unfortunately, the geological history of *Isoëtes* is exceedingly meagre, a fact which may be correlated with the almost complete absence of hard tissues (apart from the ripe spores) from the sporophyte of this genus.

We are accordingly led to the conclusion that *Isoëtes* belongs to a separate Class of Vascular Cryptogams, the Isoëtales, co-ordinate with the Filicales, Lycopodiales, Psilotales, Equisetales, and Sphenophyllales.

Summary.

The trilobed caudex of *Isoëtes japonica* consists of two distinct structures, viz. *Stem* and *Rhizophore*, to which the leaves and roots are respectively attached; but owing to the stunted growth of the plant, all external morphological differentiation between the two organs has been completely lost.

Stem.—The stem-apex has the form of a conical mass of tissue situated at the base of the funnel-shaped depression in the cortex. In this protuberance no definite apical cell can be distinguished.

Primary xylem, phloem, and cortex are differentiated from the primary meristem of the stem.

The cauline primary vascular axis is a non-medullated monostele. Primary phloem, in which true sieve-tubes occur, surrounds the central xylem-core.

An endophytic mycorrhiza is found in the peripheral cells of the primary cortex.

The cambium, which arises very early from the outermost layer of the plerome, cuts off secondary cortex externally and secondary phloem internally.

Sieve-tubes with sieve-areas of the typical cryptogamic type occur both in the primary and in the secondary phloem, and are continuous with those of the leaf-traces.

No secondary xylem is formed in *Isoëtes japonica*.

Rhizophore.—The roots, the vascular bundles of which are collateral with usually endarch protoxylem, are arranged in acropetal series upon a distinct root-bearing organ, the rhizophore, which in this genus must be regarded as an organ *sui generis*.

The primary growth of the rhizophore proceeds from a primary meristem situated along three radiating lines which correspond to the main fissures in the caudex.

The primary and secondary tissues of the rhizophore are essentially similar to the corresponding tissues of the stem.

Leaf.—The protoxylem of the collateral vascular bundle is exarch in the lamina, but becomes mesarch in the sporangial region of the leaf.

True sieve-tubes occur in the phloem of the leaf. The ligule is very well developed in *Isoëtes japonica*. It has a protective function; the young ligule envelops the younger leaves and also secretes mucilage.

Systematic.—The species of *Isoëtes* can be grouped together under two sections, Eu-Isoëtes and Cephaloceraton.

Isoëtes occupies an isolated position amongst recent Vascular Cryptogams, and is regarded as the sole living representative of the Class Isoëtales.

In conclusion, we wish to express our thanks to Professor J. B. Farmer, F.R.S., for his valuable advice and kindly criticism throughout the course of this investigation.

Postscript.

Since the foregoing was written, the first two of a series of articles by Prof. Lang, dealing with the organization of the "stock" of *Isoëtes lacustris*, have appeared *.

Although our interpretation of the general morphology of this plant agrees on the whole with that of Prof. Lang, still, his account of the development of the stelar tissues of the stem from the apical meristem cannot be reconciled with our observations.

We also differ from him in our interpretation of the mode of growth of the roots from the rhizophoric region, since we consider that there is an actual penetration of the cortex of the rhizophore by the developing roots.

Also, our conclusions as to the affinities of *Isoëtes* differ from those of Prof. Lang, who claims that this genus represents the last stage of reduction of the *Lepidodendron*-type.

Bibliography.

1. Baker, J. G.—Handbook of the Fern Allies. London, 1887.
2. Bower, F. O.—Origin of a Land Flora. London, 1908.
3. Braun, A.—Weitere Bemerkungen über *Isoëtes*. Flora, xxx. 1847.
4. —— Ueber eine neue Art der Gattung *Isoëtes*. Monatsb. der königl. Akad. d. Wiss. zu Berlin, 1861.
5. —— Zwei deutsche *Isoëtes*-Arten nebst Winken zur Aufsuchung derselben (und ein Anhang über einige ausländische Arten derselben Gattung). Verhandl. d. bot. Verein. d. Prov. Brandenb. und die angrenzend. Länd., Heft. iii., iv. Berlin, 1862; 299–333.
6. —— Bemerkungen über die *Isoëtes*-Arten der Insel Sardinien. Monatsb. der königl. Akad. d. Wiss. zu Berlin, 1863.
7. Bruchmann, H.—Ueber Anlage und Wachsthum der Wurzeln von *Lycopodium* und *Isoëtes*. Jenaische Zeitschrift f. Naturwiss. viii. 1874.
8. —— Untersuchungen über *Selaginella spinulosa*, A. Br. Gotha, 1897.

* Lang, W. H., "Studies in the Morphology of *Isoëtes*." Part 1, Mem. Proc. Manchester Lit. Phil. Soc. lix. No. 3, Feb. 1915; Part 2, *l. c.* No. 8, May 1915.

9. Butler, G. D., in G. Engelmann, "The Species of *Isoëtes* of the Indian Territory." Bot. Gaz. vol. iii. 1878.
10. Campbell, D. H.—Contributions to the Life-History of *Isoëtes*. Annals of Botany, vol. v. 1891.
10 a. —— Mosses and Ferns. 1905.
11. —— Eusporangiatæ. Carnegie Institute of Washington Publication 140. 1911.
12. De Bary, A.—Comparative Anatomy of the Phanerogams and Ferns. Oxford, 1884.
13. Eaton, A. A., in Gray's 'Manual,' ed. 7. 1908.
14. Farmer, J. B.—On *Isoëtes lacustris*. Annals of Botany, vol. v. 1890.
15. Hegelmaier, F.—Zur Kenntniss einiger *Lycopodium*. Bot. Zeitung, xxxii. 1874.
16. Hofmeister, W.—Germination, Development, and Fructification of the Higher Cryptogamia. Ray Soc. London, 1862.
17. Janczewski, E. de.—Études comparées sur les Tubes cribreux. Ann. Sci. Nat. Bot. sér 6, xiv. 1882.
18. Janse, J. M.—Les Endophytes radicaux de quelques Plantes Javanaises. Ann. du Jard. Bot. de Buitenzorg, xiv. 1897.
19. Kruch, O.—Istologia ed istogenia del fascio conduttore delle foglie di *Isoëtes*. Malpighia, iv. 1890.
20. Lang, W. H.—On the Stock of *Isoëtes*. Report of the British Association for the Advancement of Science, Sheffield, 1910.
21. Lotsy, J. P.—Vorträge über botanische Stammesgeschichte, Bd. ii. 1909.
22. Makino, T.—Observations on the Flora of Japan. Tôkyô Bot. Mag. xviii. 1904.
23. Milde, J.—Filices Europæ Atlantidis, Asiæ Minoris et Sibiriæ. Leipzig, 1867.
24. Mohl, H. von.—Ueber den Bau des Stammes von *Isoëtes lacustris*. Linnæa, xiv. 1845.
25. Motelay, L., et A. Vendryés.—Monographie des Isoëteæ. Actes de la Soc. Linn. de Bordeaux, xxxvi. 1882.
26. Russow, E.—Vergleichende Untersuchungen der Leitbündel-Kryptogamen. Mém. de l'Acad. Imp. des Sciences de St. Pétersbourg, sér. 7, xix. 1872.
27. Sadebeck, R.—Isoëtaceæ in Engler u. Prantl, Natürliche Pflanzenfamilien, i. Abt. iv. 1902.
28. Scott, D. H., and T. G. Hill.—The Structure of *Isoëtes Hystrix*. Annals of Botany, vol. xiv. 1900.
29. Seward, A. C., and S. O. Ford.—The Anatomy of *Todea*, with Notes on the Geological History and Affinities of the Osmundaceæ. Trans. Linn. Soc. Lond., Bot. vi., 1903, pp. 237–260, tt. 27–30.
30. Smith, R. Wilson.—The Structure and Development of the Sporophylls and Sporangia of *Isoëtes*. Bot. Gaz. vol. xxix. 1900, pp. 225–258, 323–346, tt. 13–20.
31. Solms-Laubach, H. Graf zu.—Ueber das Genus *Pleuromeia*. Bot. Zeitung, lvii. 1899.
32. Stokey, A. G.—The Anatomy of *Isoëtes*. Bot. Gaz. vol. xlvii. 1909.
33. Van Tieghem, Ph.—Traité de Botanique, ed. 1. 1884.
34. —— Traité de Botanique, ed. 2. 1891.
35. Vines, S. H.—The Systematic Position of *Isoëtes*. Annals of Botany, vol. ii. 1889.
36. Yapp, R. H.—*Spiræa Ulmaria*, L., and its Bearing on the Problem of Xeromorphy in Marsh Plants. Annals of Botany, vol. xxvi. part 2. 1912.
37. Zenetti, P.—Das Leitungssystem im Stamm von *Osmunda regalis*, L. Bot. Zeitung, liii. 1895.

Explanation of Abbreviations.

c. = cambium.
cel.l. = cellulose layer.
ct. = cortex (*ct.p.* = cortical parenchyma).
cut. = cuticle.
cut.l. = cuticularized layer.
gr^1, gr^2. = main furrow, secondary furrow.
l. = leaf.
l.t. = leaf-trace.
lig. = ligule.
lig.sh. = ligular sheath.
m. = mantle.
mer. = meristem (primary).
n. = nucleus.
p. = parenchyma.
per. = periderm.
$ph.^1$, $ph.^2$ = primary phloem, secondary phloem (*ph.p.* = phloem parenchyma).
pler. = plerome.
pr.x. = protoxylem.
ps.e. = pseudo-endodermis.
r. = root.
rh. = rhizophore.
r.t. = root-trace.
s. = stem.
s.t. = sieve-tube.
tr. = tracheid.
v. = vesicle.
x. = xylem (x^1 = primary xylem, x^2 = secondary xylem).
x.p. = xylem parenchyma.

EXPLANATION OF PLATES 33–40.

Plate 33.

Figs. 1–3. From transverse sections of the caudex, showing successive stages in the formation of a main furrow.
a = cells without starch, probably phellogen;
b = cells with suberized walls (= periderm).
In all three figures the left-hand side is towards the centre of the stem. Figs. 1 & 2 × 220; fig. 3 × 100.

Fig. 4. Lateral view of a fairly old caudex. Nat. size.

Fig. 5. Caudex of a young plant (about two years old) viewed from below. Some of the roots have been removed in order to show their arrangement on the caudex. Nat. size.

Fig. 6. Lateral view of the same specimen. The leaves and roots have been completely removed. Nat. size.

Fig. 7. A median longitudinal section of a plant about four years old. × 1·5.
a = present season's growth;
b = groups of stretched cortical cells.

Fig. 8. Central portion of the same section magnified five diameters.

Plate 34.

Fig. 9. Longitudinal section through the caudex represented in figs. 5 & 6. The plane of the section is shown by the dotted line α ..... β in fig. 5. × 2·3.

Fig. 10. Apical portion of the same section (diagrammatic). Since this section is not strictly median, it does not pass through the actual apex of the stem. Note at *x* the early differentiation of the stelar tracheids. × 45.

Fig. 11. Part of the same section, including the basal portion of the uppermost leaf-trace (on the left) and the adjacent stelar tissues. × 250.
Compare the size and shape of tracheids belonging to the leaf-trace and stele respectively.

Fig. 12. Slightly oblique transverse section of a stem passing through the youngest part of the stele. × 250. Note the leaf-traces surrounding the stelar region, many of which are not yet differentiated.

Fig. 13. Part of a transverse section through the oldest part of the caudex showing connection of leaf-trace with stem-stele. × 200.

Plate 35.

Fig. 14. Ditto, showing the horizontally stretched xylem parenchyma of the stem-stele. × 220.

Fig. 15. Part of a tangential section of the stem (cut in a plane immediately outside the stele) showing several leaf-traces cut transversely. × 220.
The phloem of the leaf-traces is shown in organic connection with that of the stem-stele.
Note the deposits of callus.

Fig. 16. A similar section of the stem of *Isoëtes lacustris*. × 285.

Fig. 17. Part of a sieve-tube from the root, showing sieve-areas on the lateral walls. × 700.

Figs. 18 & 19. Sieve-tubes of the secondary phloem; from a transverse section of the stem. × 700.
Note the callus deposited in some of the cells.

Fig. 20. Sieve-tubes of the secondary phloem of *Isoëtes lacustris*; from a longitudinal section of the stem. × 700.

Fig. 21. Part of a transverse section of the stem, passing through the junction of a leaf-trace with the stele. × 220. Note the phloem of the leaf-trace in direct organic connection with that of the stem.

Plate 36.

Fig. 22. Transverse section through epidermis of the submerged portion of a leaf. × 450.

Fig. 23. Transverse section through epidermis of the aerial portion of a leaf. Two stomata are shown. × 450.

Fig. 24. Stoma in surface view. × 220.

Figs. 25 & 26. Basal portion of two sporophylls from the intermediate region of the 'rosette.' Nat. size.

Fig. 27. Basal portion of one of the innermost leaves of the 'rosette.' Nat. size.

Fig. 28. Stellate cells from leaf diaphragm. × 220.

Fig. 29. A cell of the ligule. × 1000. Note the mucilaginous appearance of the cytoplasm.

Fig. 30. Transverse section of the central region of a ligule. × 100. Note the irregularly arranged cells and intercellular spaces, both of which may contain mucilage.

Fig. 31. Part of the above more highly magnified. × 220.

Fig. 32. Cells of the central region of the ligule in surface view. × 220. Note the characteristic intercellular spaces in the epidermis.

Fig. 33. Fully developed ligule. × 6.

Fig. 34. Marginal portion of the above more highly magnified. × 100.

Figs. 35–40. Successive stages in the development of the ligule. × 285.

Fig. 41. Part of a transverse section of a leaf showing the large clear cells abutting on a lacuna. × 285.

Fig. 42. Endodermis-like cells surrounding the glossopodium. × 220.

Plate 37.

Fig. 43. Sieve-tubes from a leaf-trace embedded in the cortex. × 350. Note deposition of callus on the walls.

Fig. 44. Sieve-tubes from the vascular bundle in a leaf. × 450.

Fig. 45. Sieve-tube from the vascular bundle in a leaf of *Isoëtes lacustris*. × 450.

Figs. 46–48. Series of transverse sections of the vascular bundle of a young leaf. All × 285.

Fig. 46 is drawn from a section from the middle region of the leaf;

Fig. 47 is drawn from a section at some distance from the glossopodium;

Fig. 48 is drawn from a section just above the glossopodium.

Fig. 49. Longitudinal section of the central canal of a leaf. × 450. Note the remains of the lignified bars of the end wall.

Fig. 50. A complete end wall of a central canal in surface view. × 1000. Note the lignified reticulum and the middle lamella seen through the pits.

(From a very young leaf.)

Fig. 51. Tracheids of a leaf-bundle, showing the very oblique terminal walls. × 225.

Figs. 52 & 53. Young leaves of *Isoëtes lacustris* from the centre of a leaf-rosette, showing vaginæ of the older leaf, completely enveloping the younger leaf. × 1·5.

Fig. 54. Longitudinal section of an old leaf-trace embedded in the cortex. × 100.

Between the tracheids notice the parenchymatous cells, several of which have recently undergone division.

Plate 38.

Figs. 55–59. Successive series of transverse sections of an old caudex:

Fig. 55 is cut just above the apical meristem, while

Fig. 59 is cut very near the base of the caudex. Slightly magnified.

Fig. 60. Cell from near the periphery of the primary cortex. × 500. The starch-grains have disappeared, leaving alveolar protoplasm to which numerous small proteid granules are attached. Notice the collenchymatous cell-wall.

Fig. 61. Cell of the periderm with mycorrhiza. × 500. Note intercalary and terminal vesicles.

Fig. 62. Part of a transverse section of the stem of *Isoëtes lacustris* × 200.

Fig. 63. Part of a longitudinal section of the rhizophore showing apical region of rhizophore stele. × 160.

Fig. 64. Part of a transverse section of the stem showing the peripheral tissues of the stem-stele. × 280.

Plate 39.

Figs. 65–70. Median longitudinal sections through the growing-point of the stem. All × 320.

Fig. 65. An old plant of *I. lacustris*.

Fig. 66. A very young plant of *I. lacustris*.

Fig. 67. An old plant of *I. Hystrix*.

Fig. 68. An old plant of *I. velata*.

Fig. 69. An old plant of *I. japonica*.

Fig. 70. A very young plant of *I. japonica*.

Fig. 71. Surface view of the growing-point of the stem of *Isoëtes japonica*. × 320. Drawn from a thick hand-section cleared with 'Eau de Javelle.'

Fig. 72. Surface view of the growing-point of the stem of *Isoëtes lacustris*. × 320. Drawn from a microtomed section.

Plate 40.

Fig. 73. Longitudinal section through the apex of a dichotomizing root. × 50.

Fig. 74. Secondary phloem from a transverse section of an old stem. × 200. Note sieve-fields and deposits of callus.

Fig. 75. Median longitudinal section through the stele of a very young plant. The plane of this section is at right angles to that of a main furrow. × 165.

Fig. 76. Secondary phloem from a transverse section of an old stem. × 190. Note deposits of callus.

Fig. 77. Transverse section through the lower half of one of the lobes of the rhizophore-stele. This section is cut near the apex of the lobe. × 165.

Note how the cambium (seen above and below) is interrupted by the apical meristem (*mer.*) of the rhizophore. The arrow points towards the lower surface of the stelar lobe.

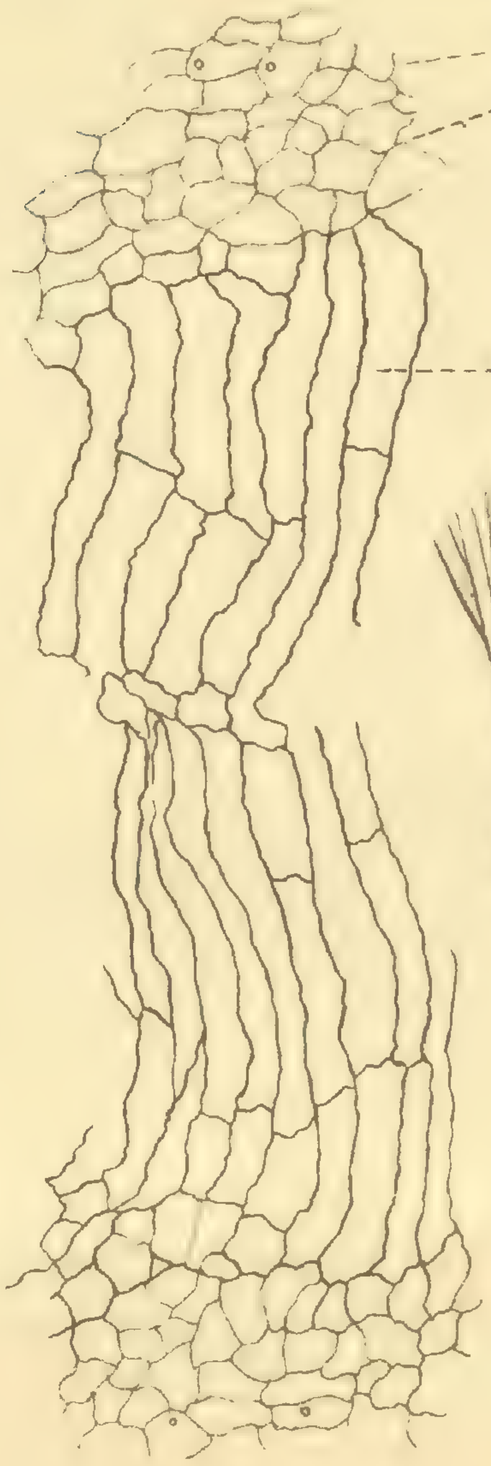
Fig. 78. Transverse section of the stele of an old stem. × 23.

Fig. 79. Transverse section of the stele in the transitional region between stem and rhizophore. × 45.

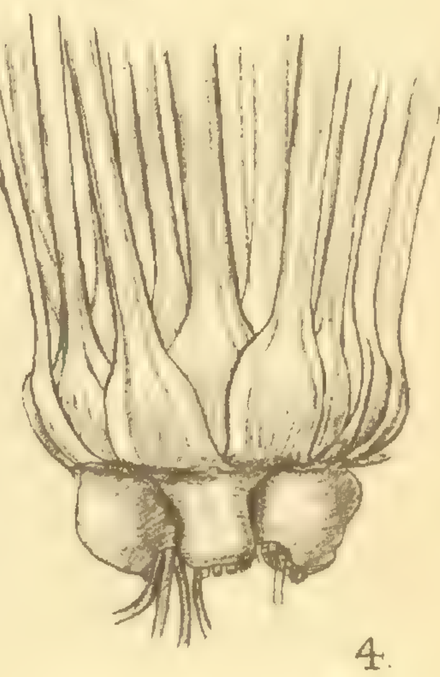
Fig. 80. Transverse section of the stele of the rhizophore. × 40.

1.

2.



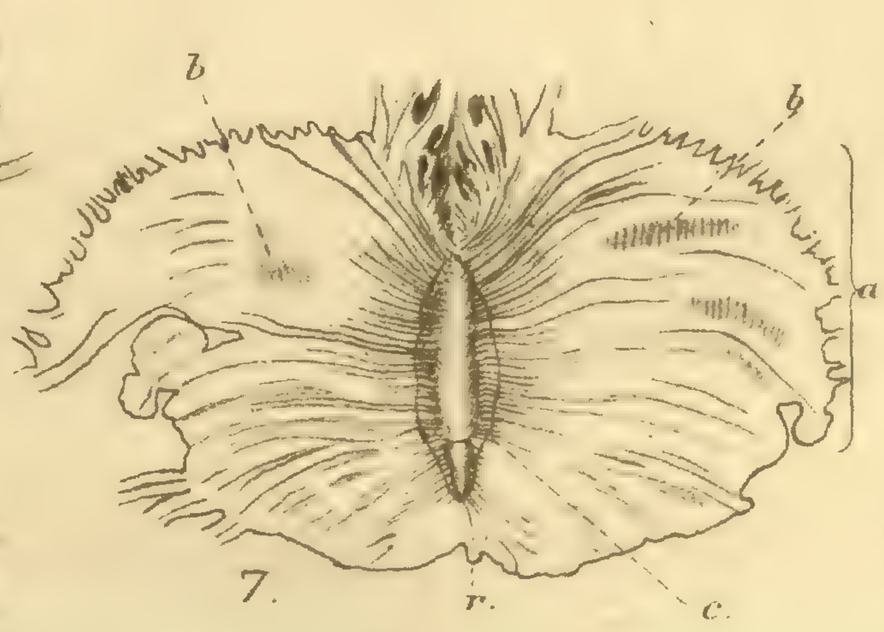
3.



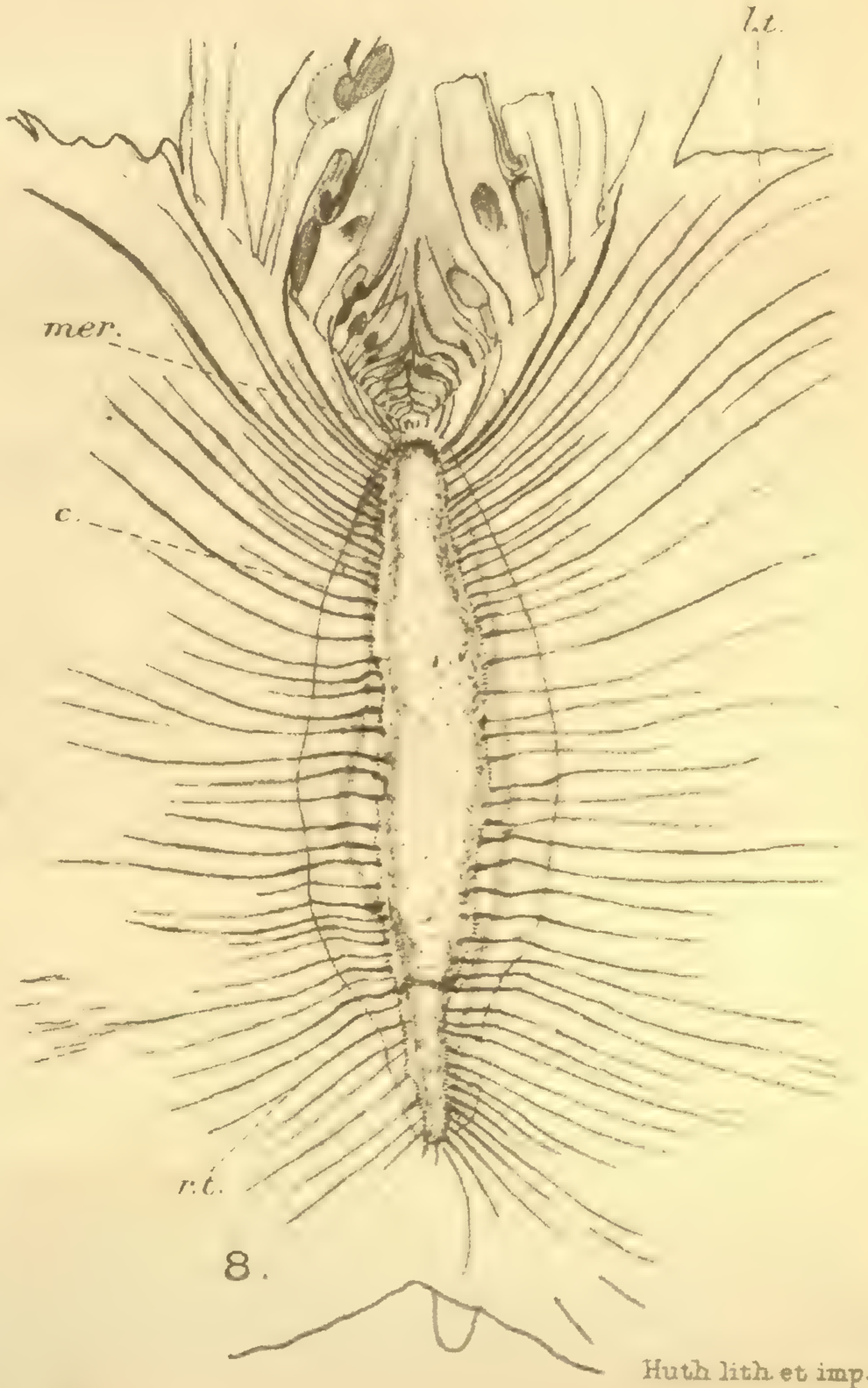
4.

5.

6.



7.

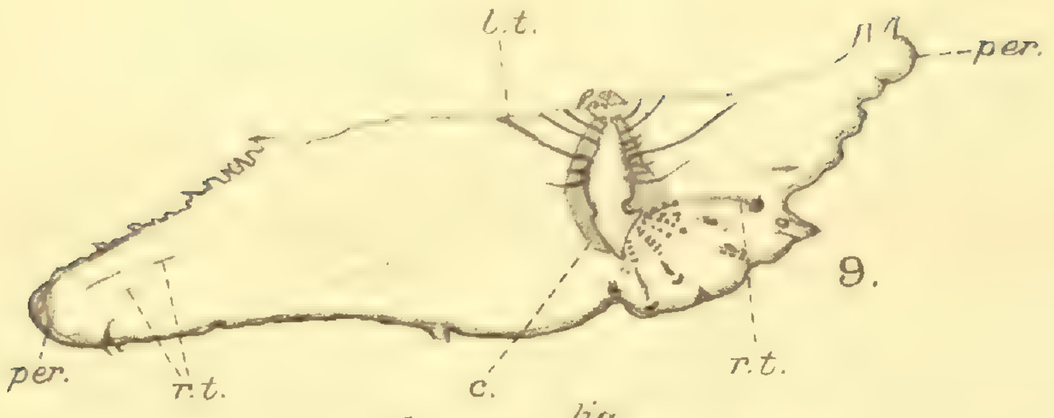


8.

H.T. del. ad nat.

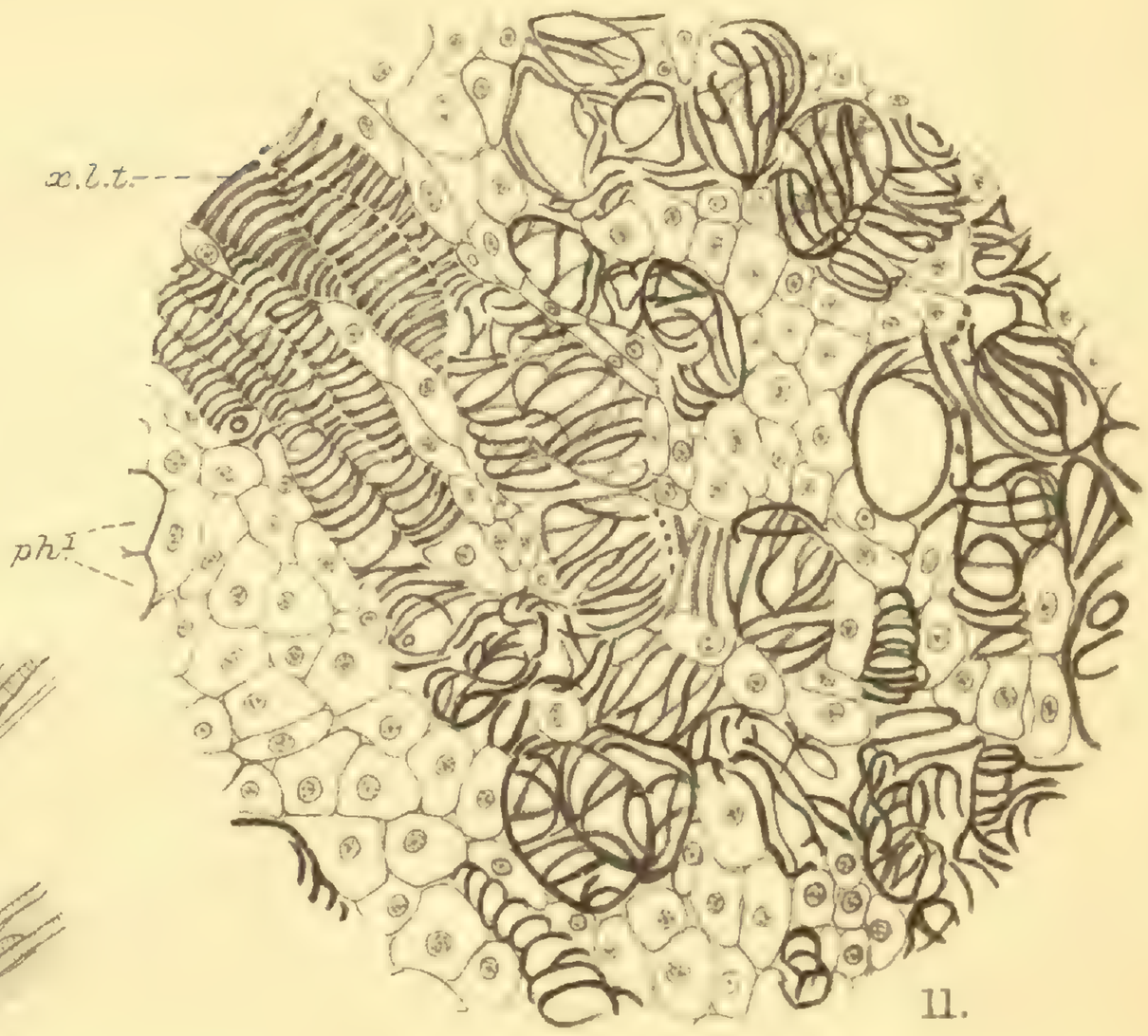
Huth lith. et imp.

ISOETES JAPONICA, A. Br.



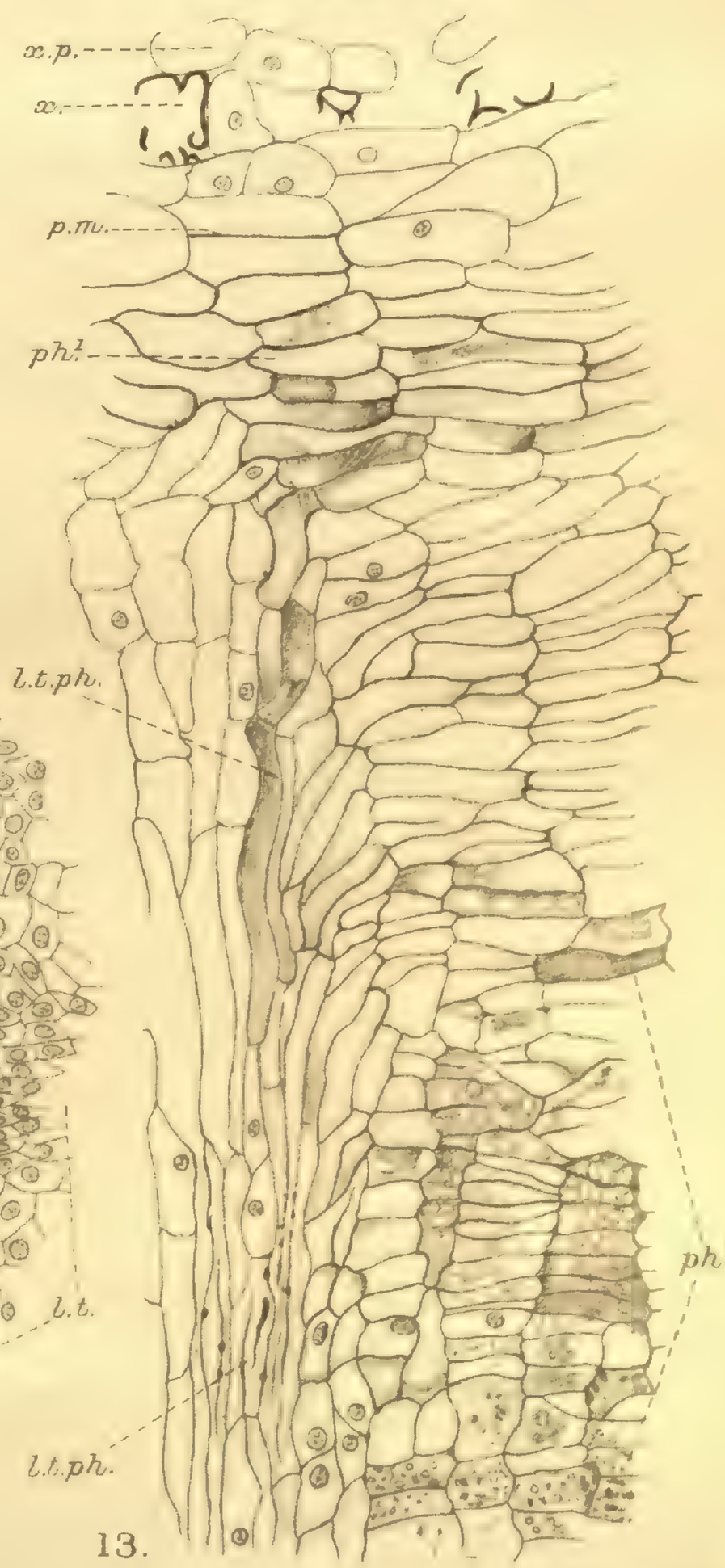
9.

10.



11.

12.

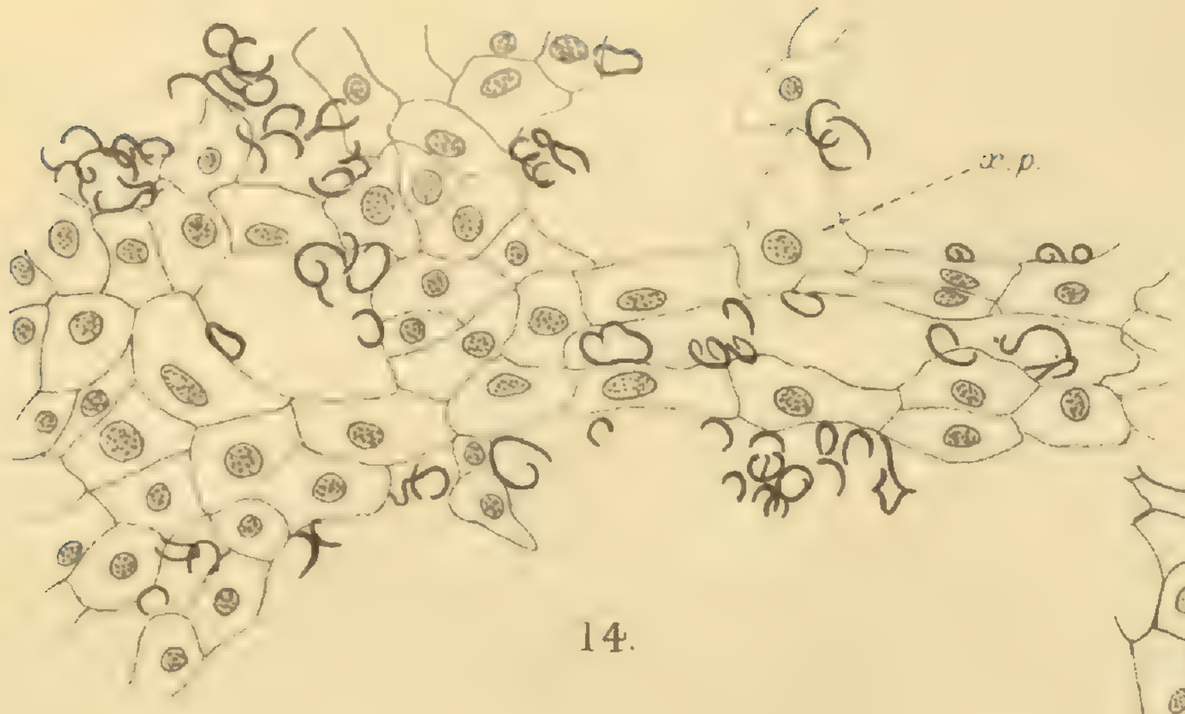


13.

H.T. et C.W. del. ad nat

Huth lith. et imp.

ISOETES JAPONICA, A. Br.



14.

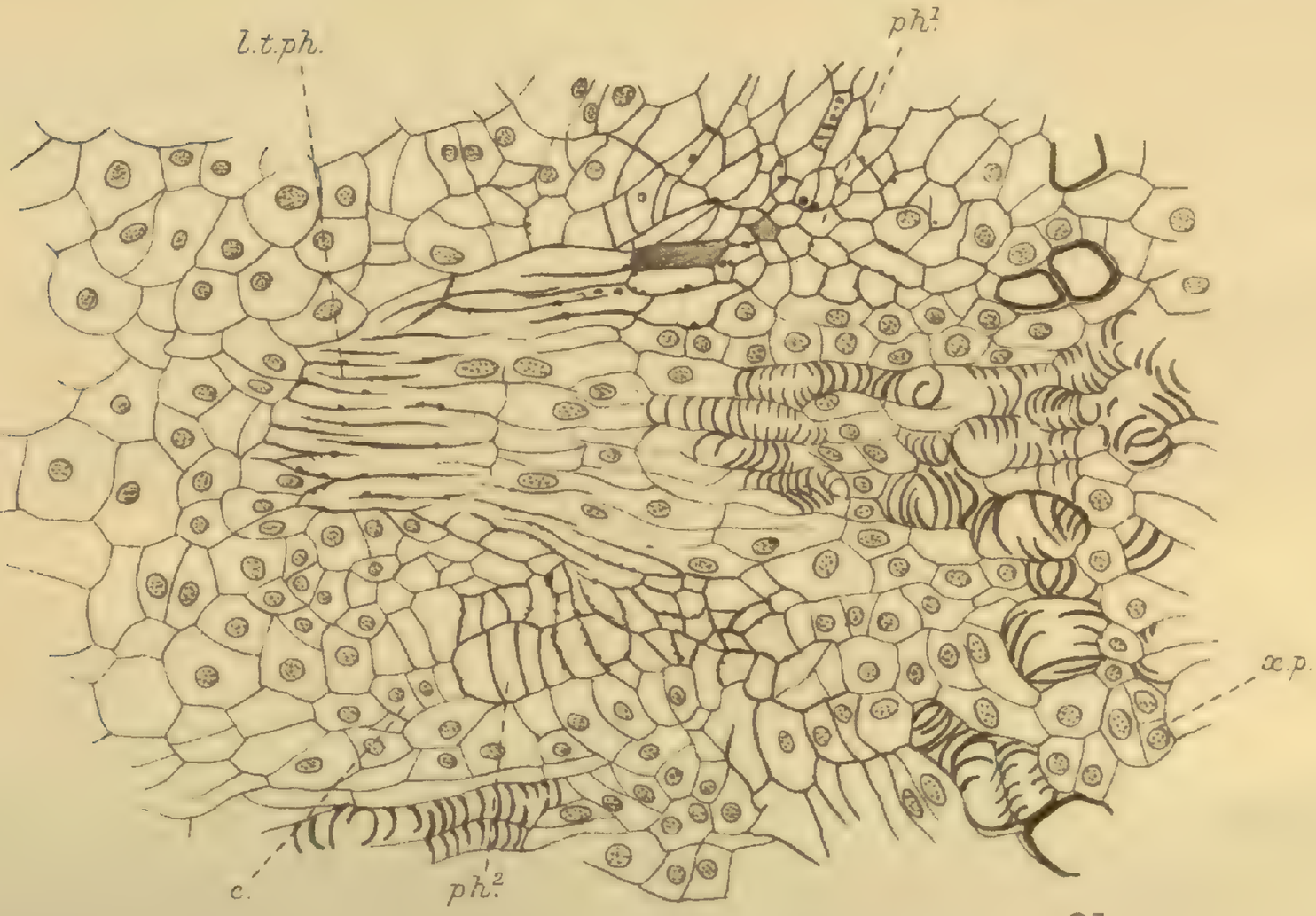
15.

16.

17.

18.

19.



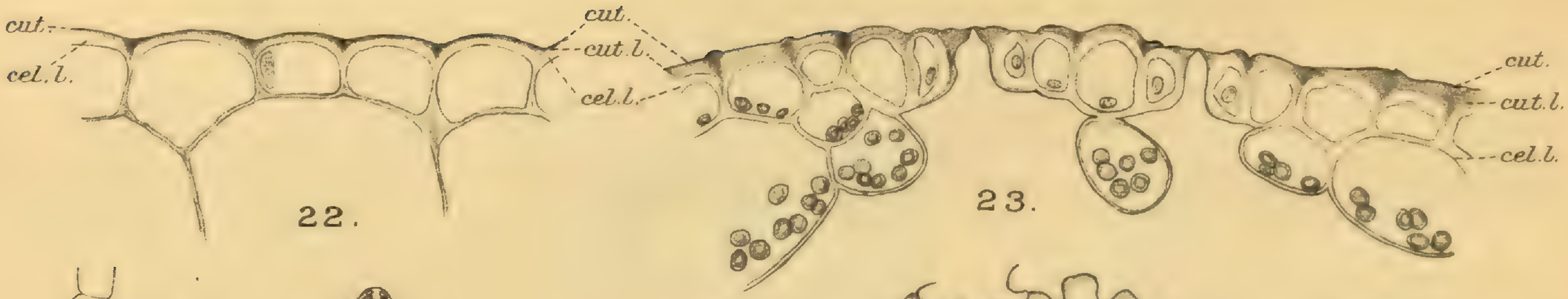
21.

20.

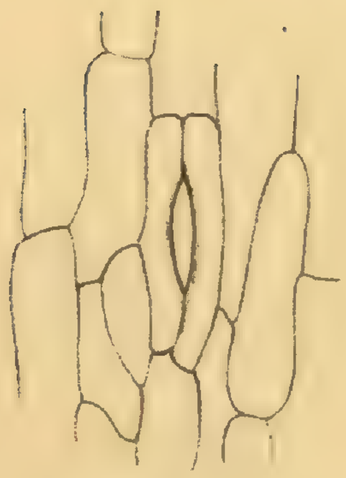
H.T. del. ad nat.

Huth lith. et imp.

ISOETES JAPONICA, A. Br.



22. 23.

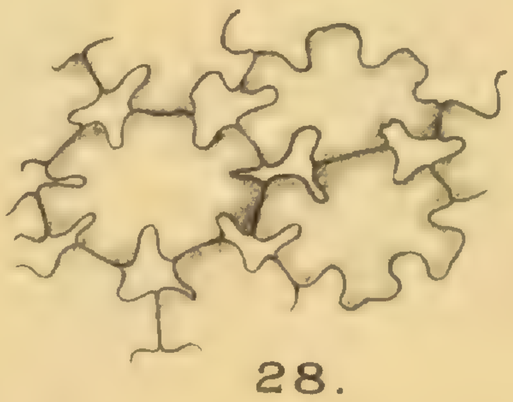


24.

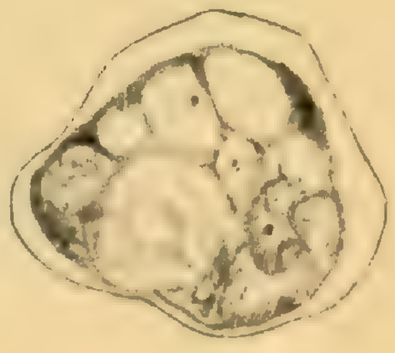
25.

26.

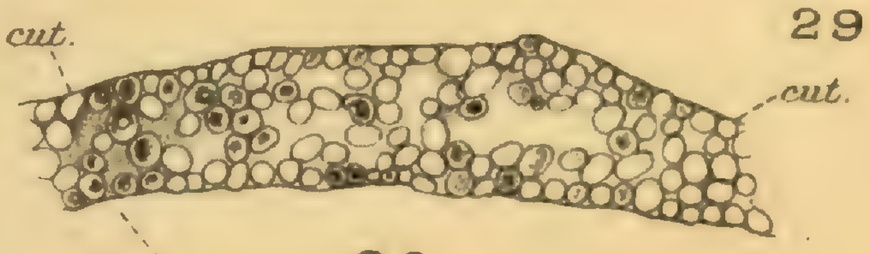
27.



28.

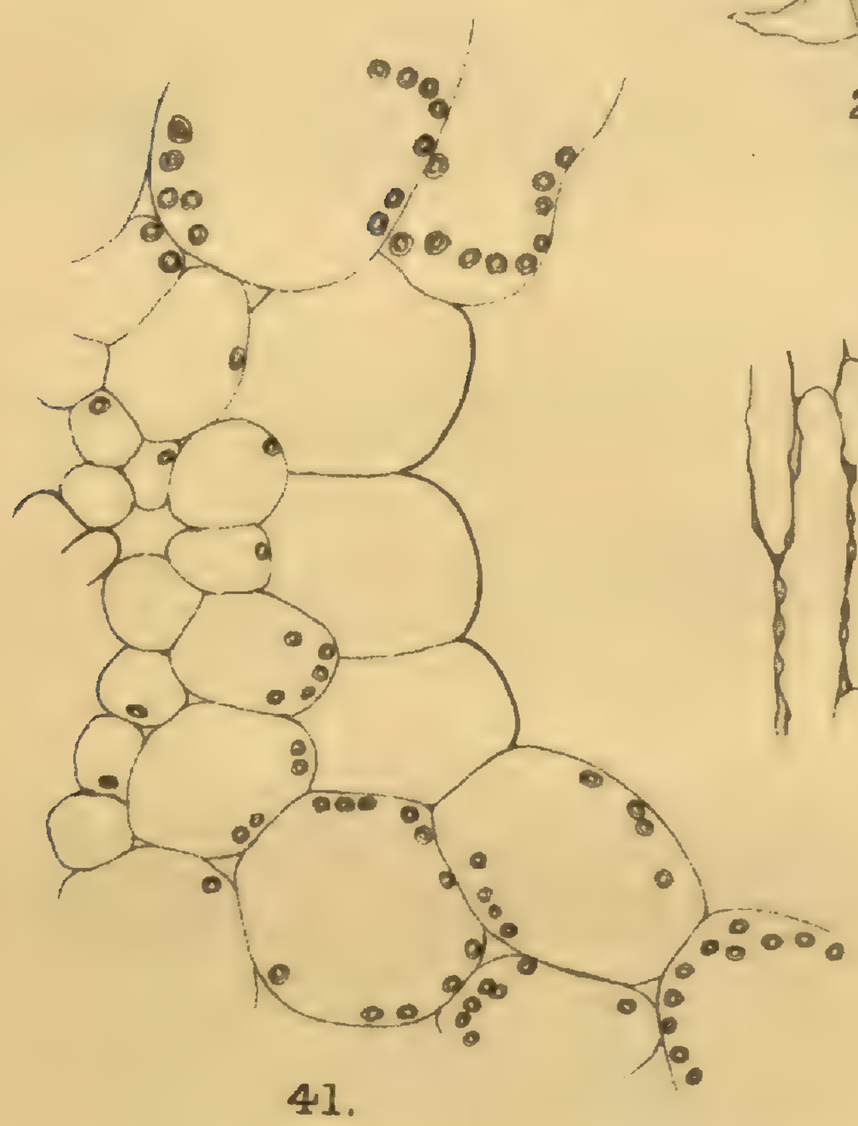


29.

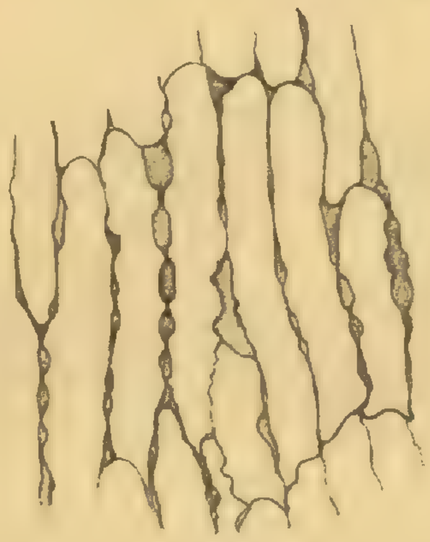


30.

31.



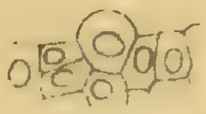
41.



32.

33.

34.



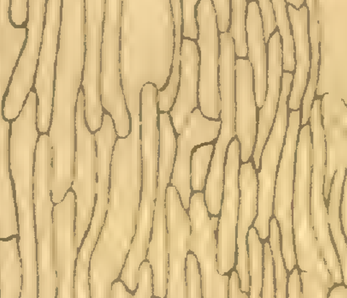
35.

36.

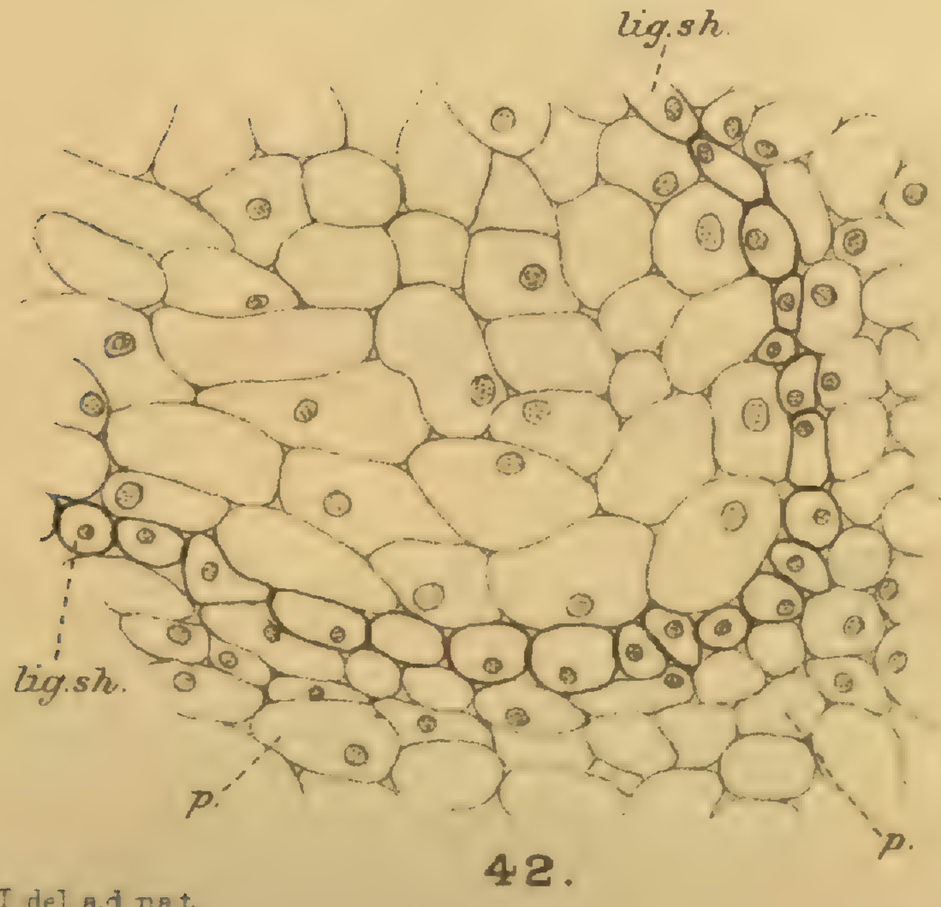
38.

37.

39.



40.

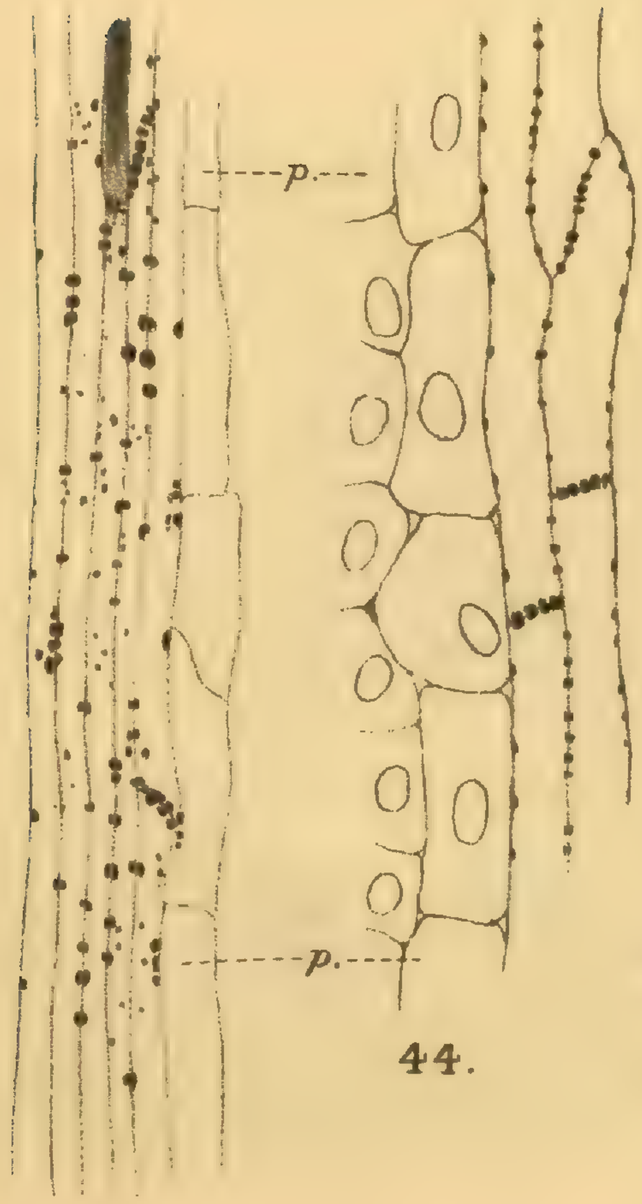


42.

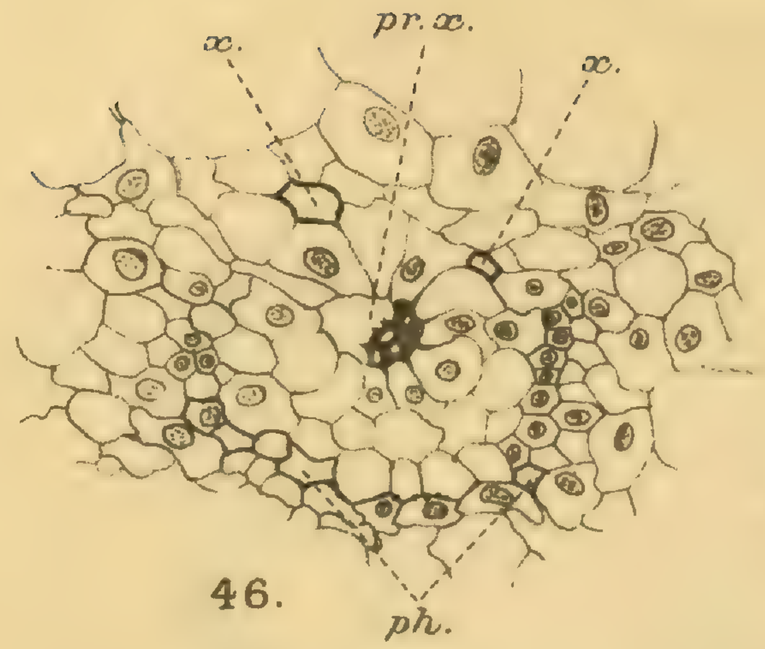
H.T del ad nat.

Huth lith et imp.

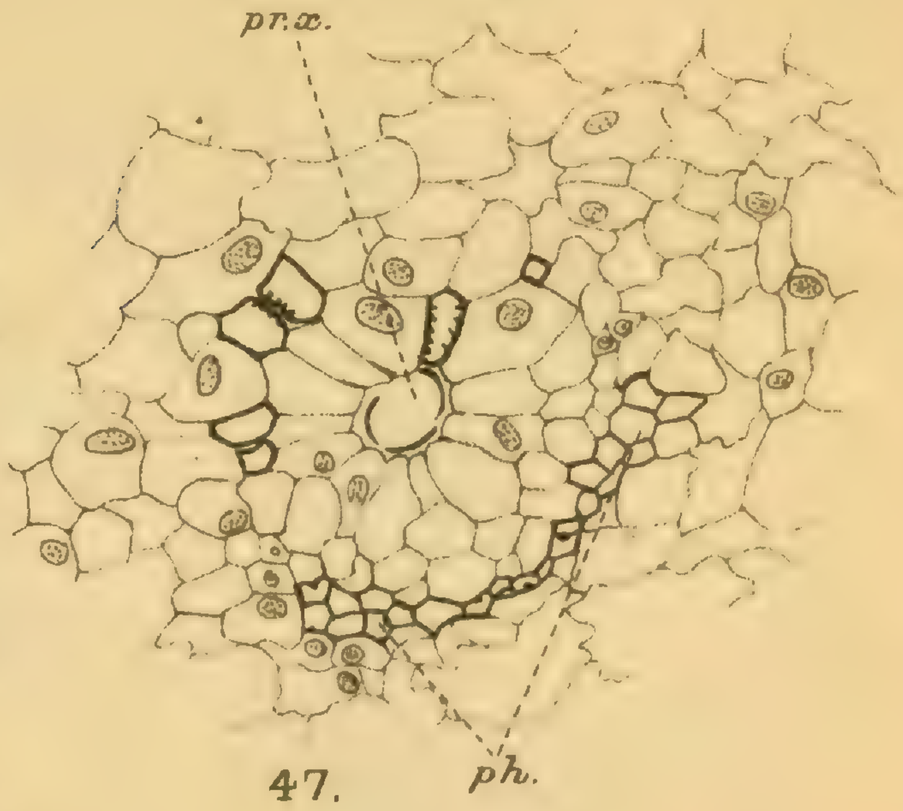
ISOETES JAPONICA, A.Br.



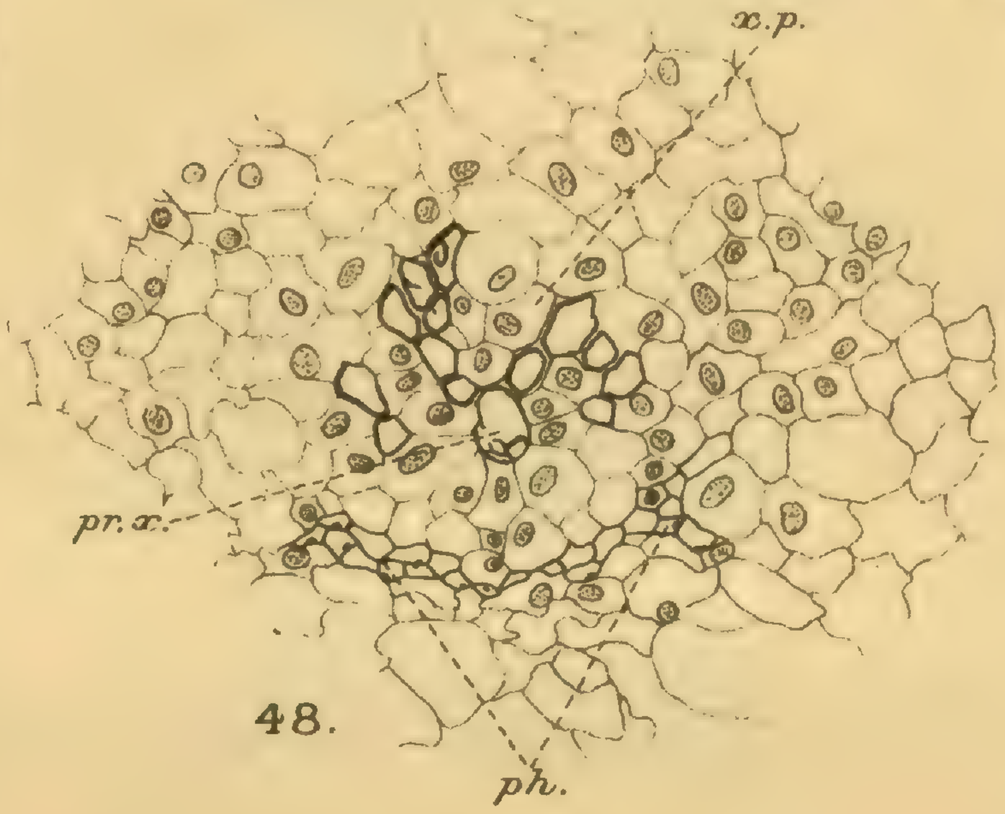
43. 44.



46.

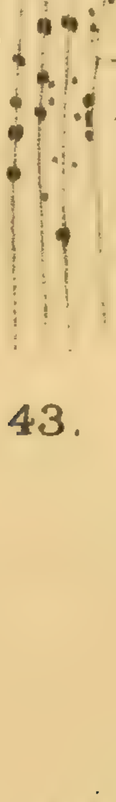


47.

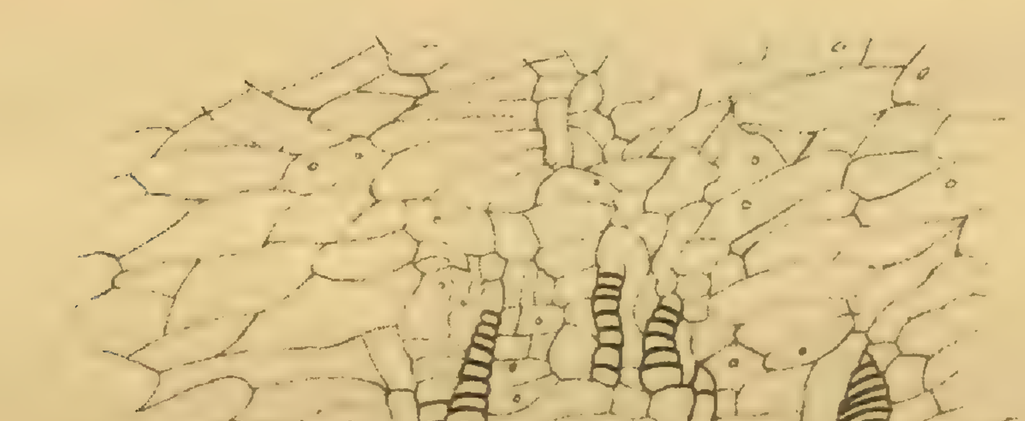


48.

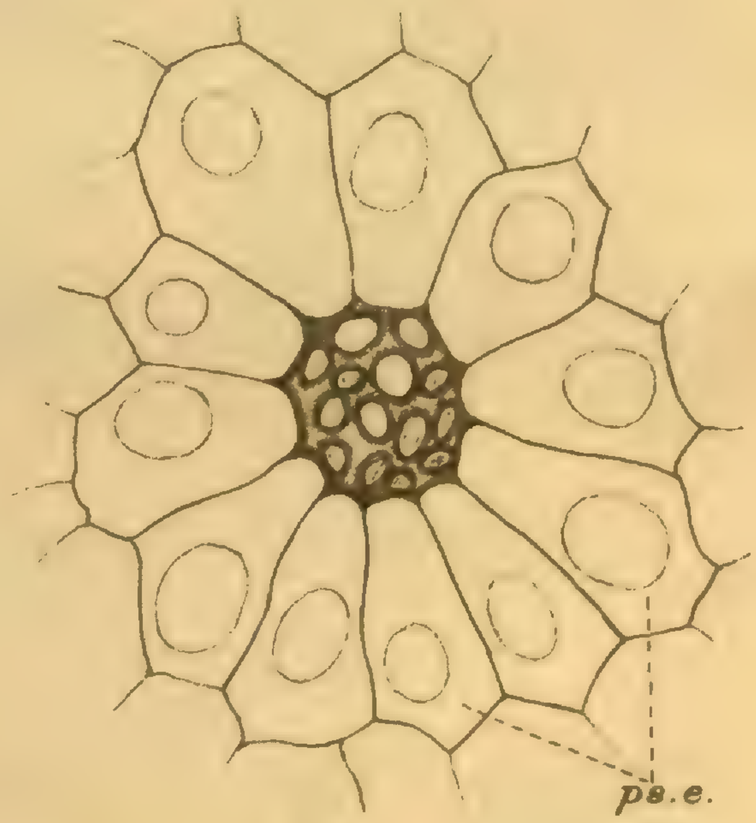
49.



45.



54.



50.

53.

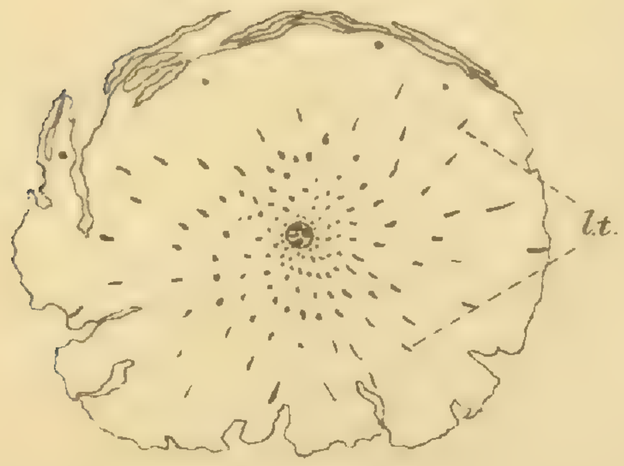
52.

51.

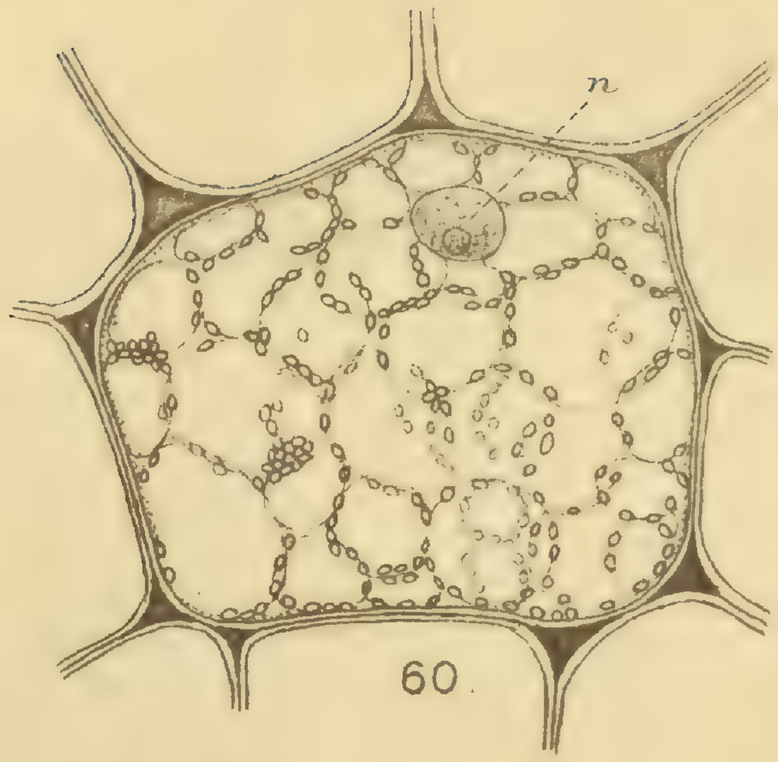
H.T. del. ad nat.

Huth lith. et imp.

ISOETES JAPONICA, A. Br.

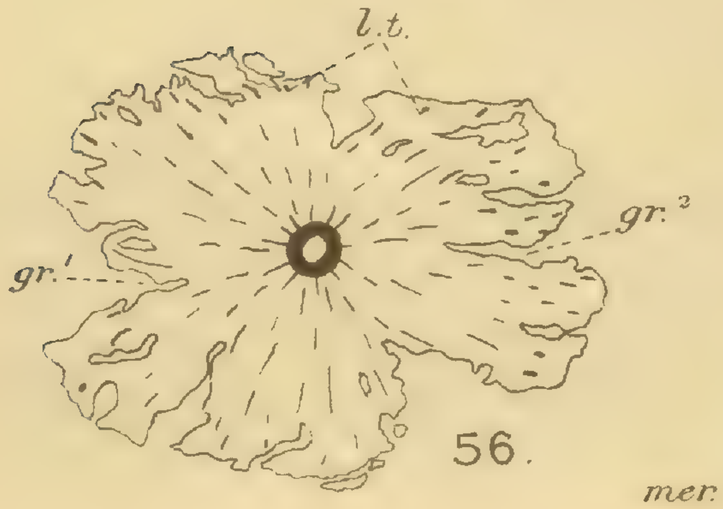


55.

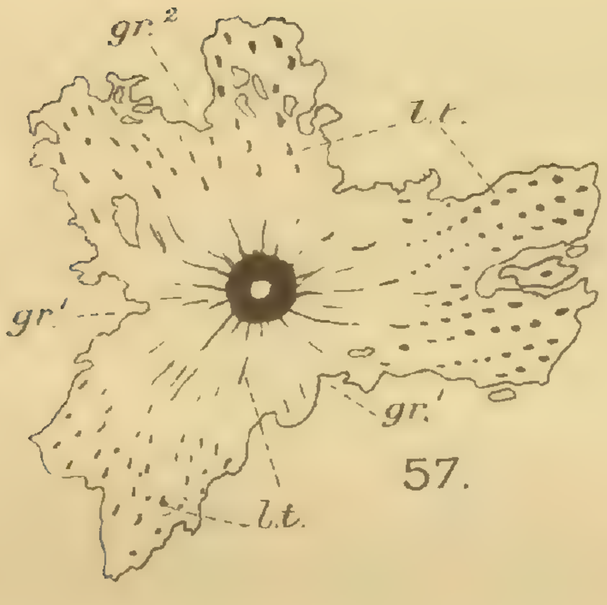


60.

61.

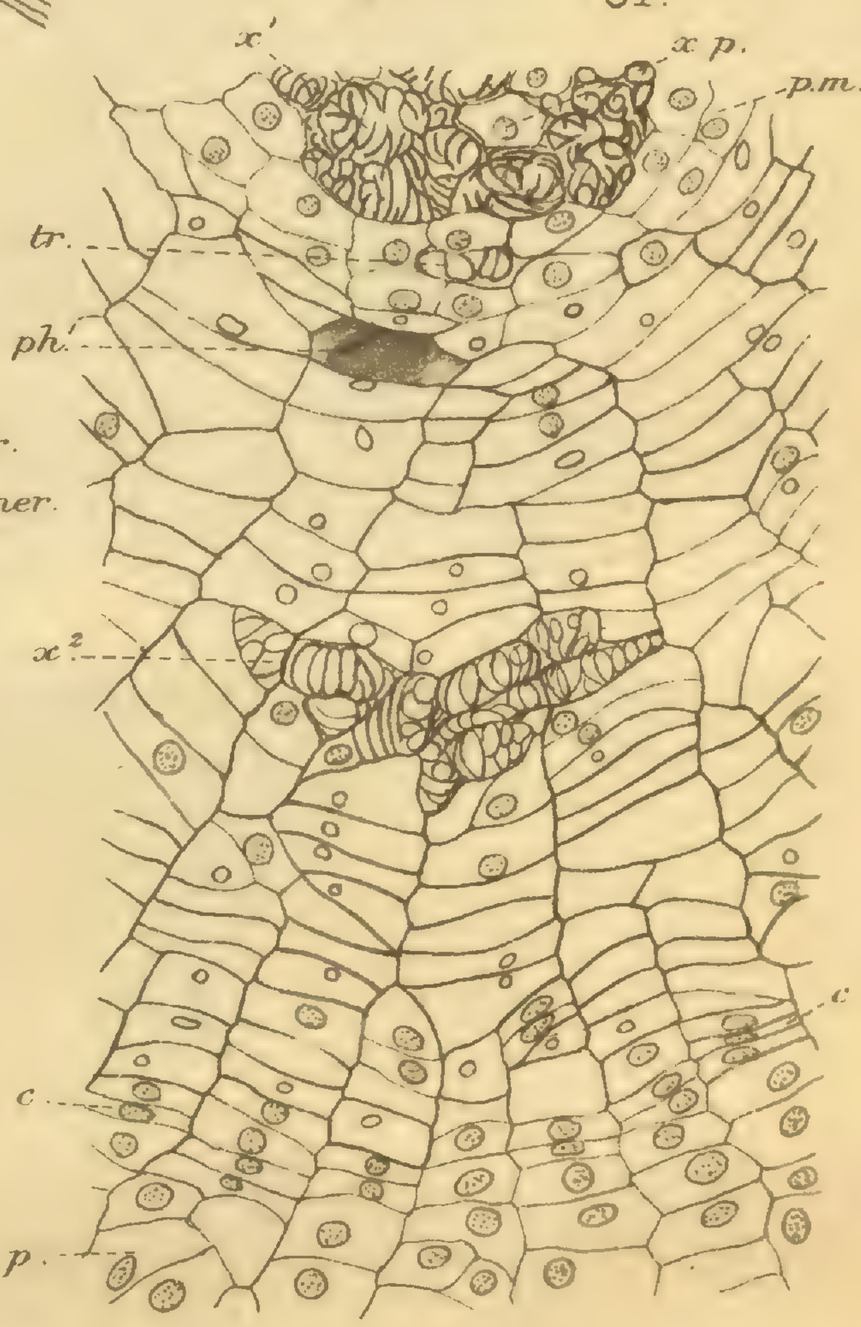


56.

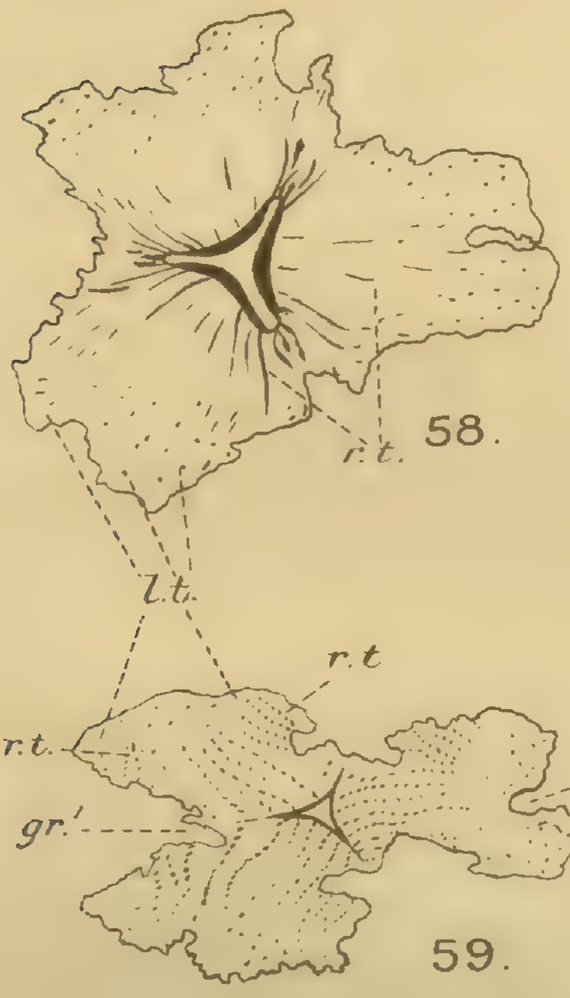


57.

63.

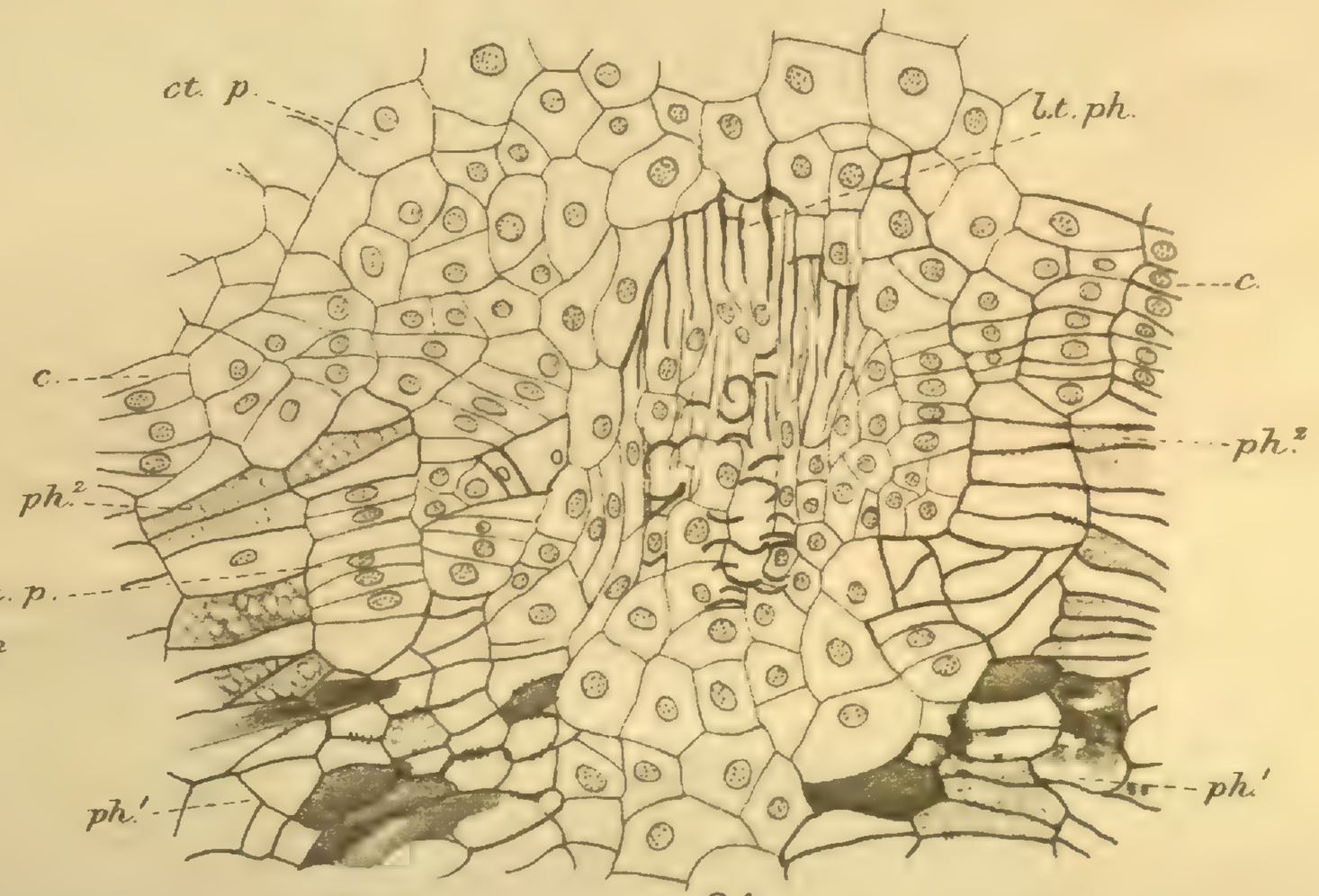


62.



58.

59.

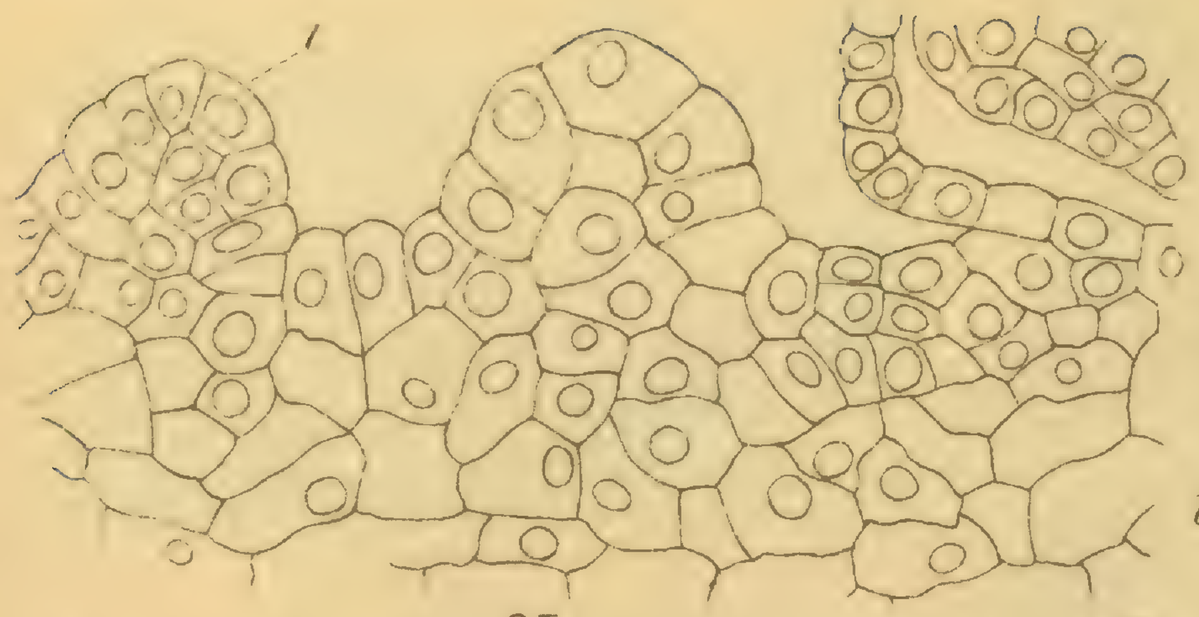


64.

C.W et H.T. del. ad nat.

Huth lith. et imp.

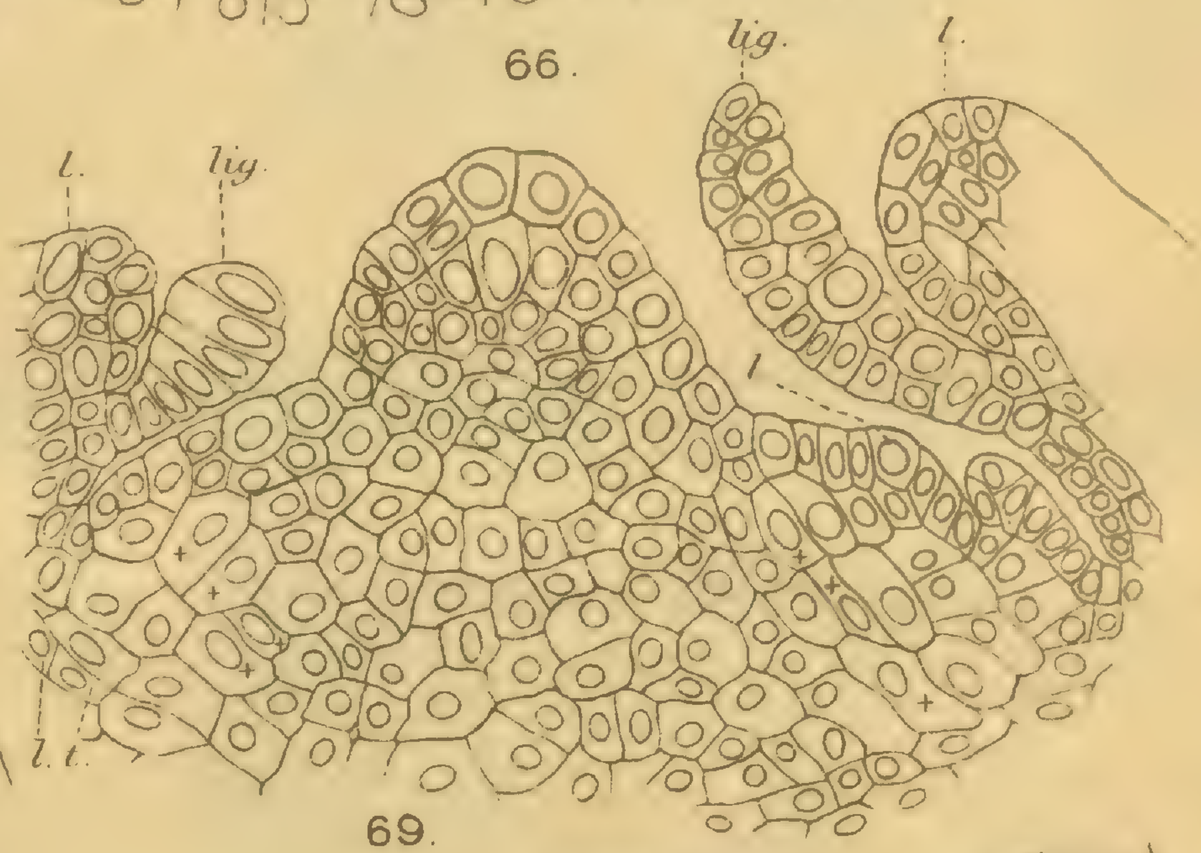
ISOETES JAPONICA, A. Br.



65.

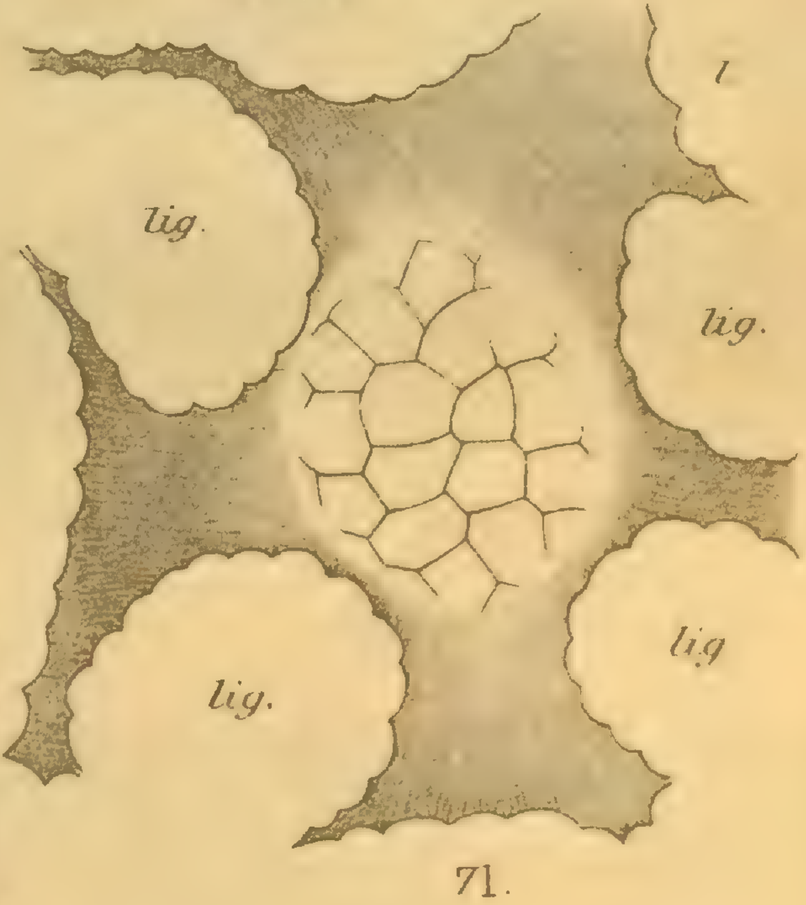
66.

67.

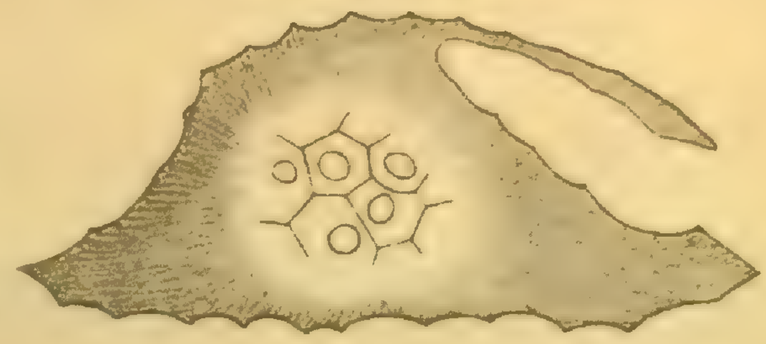


69.

68.



71.



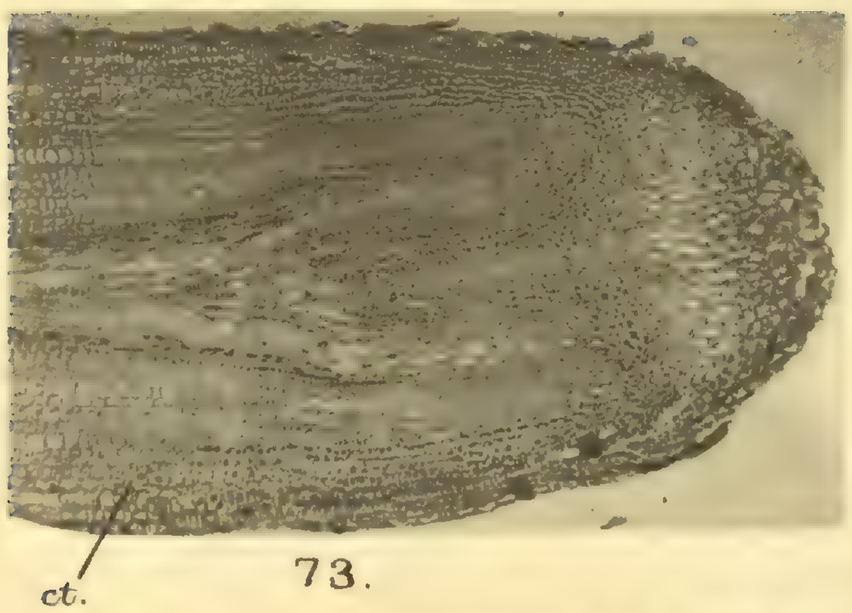
72.

70.

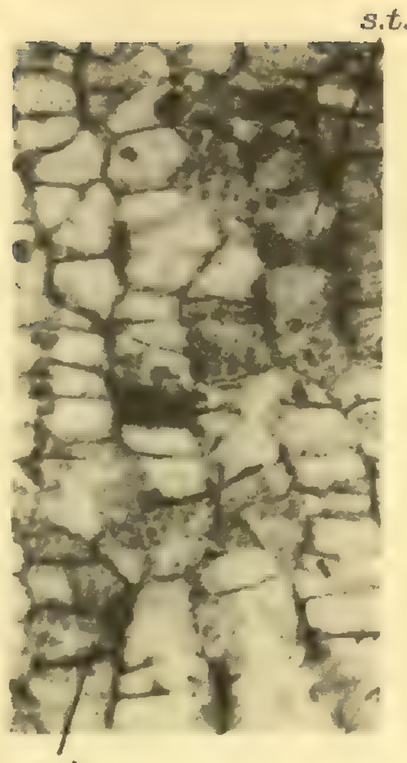
H.T del. ad nat.

Huth lith. et imp.

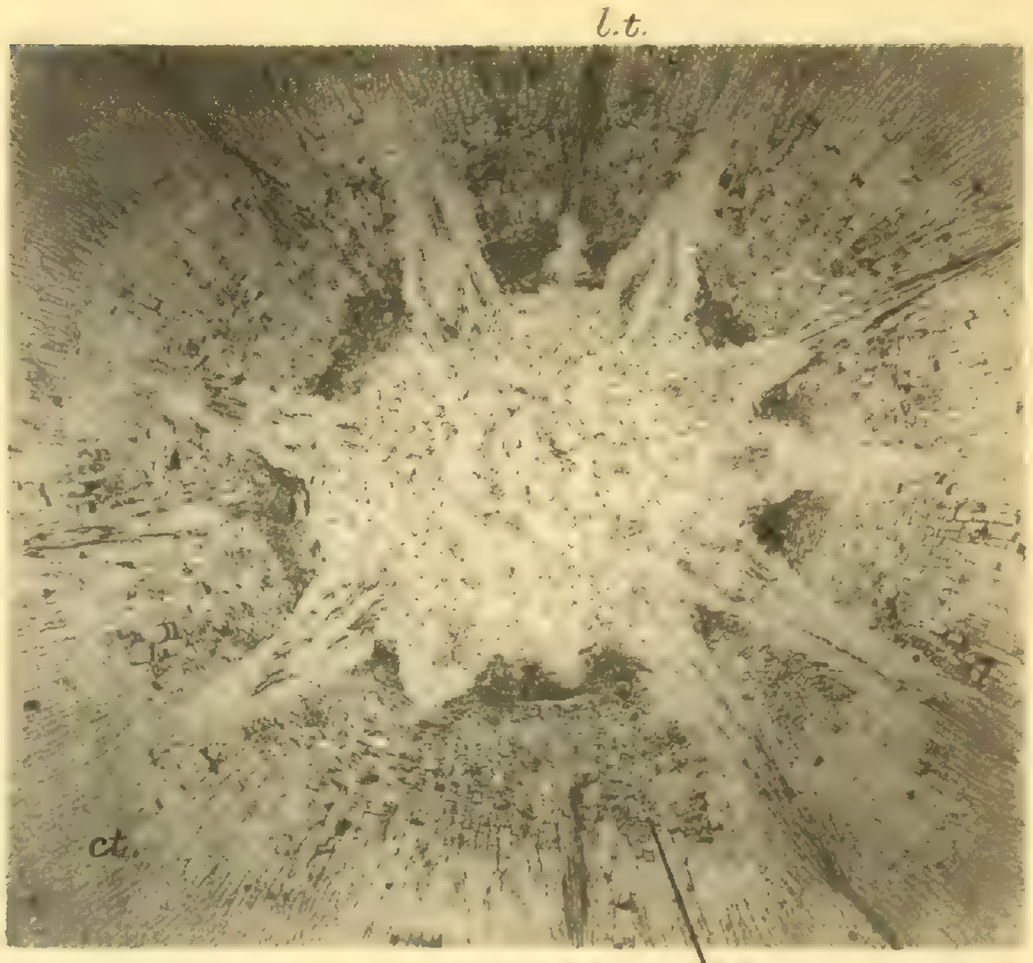
ISOETES JAPONICA, A. Br.



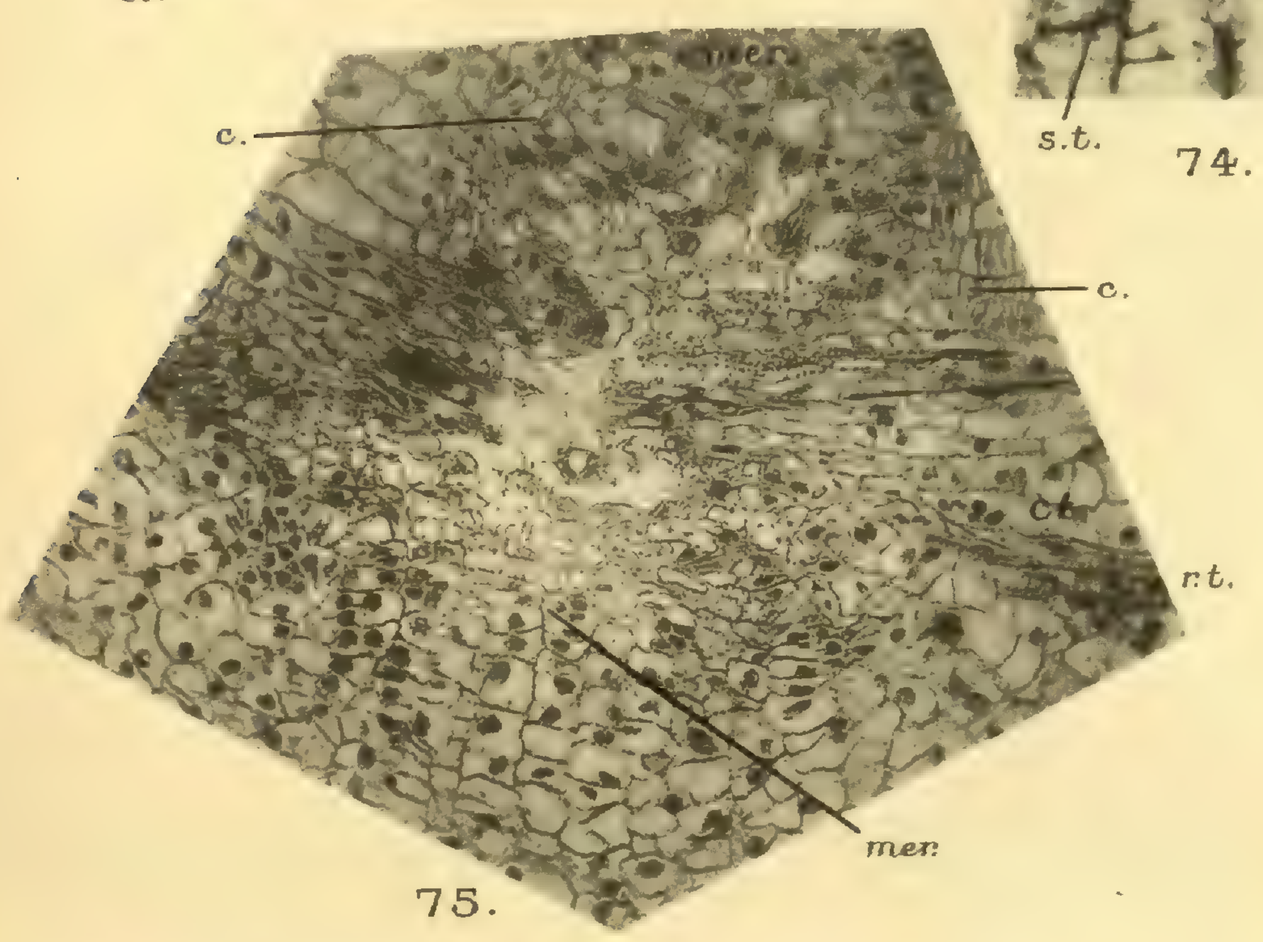
73.



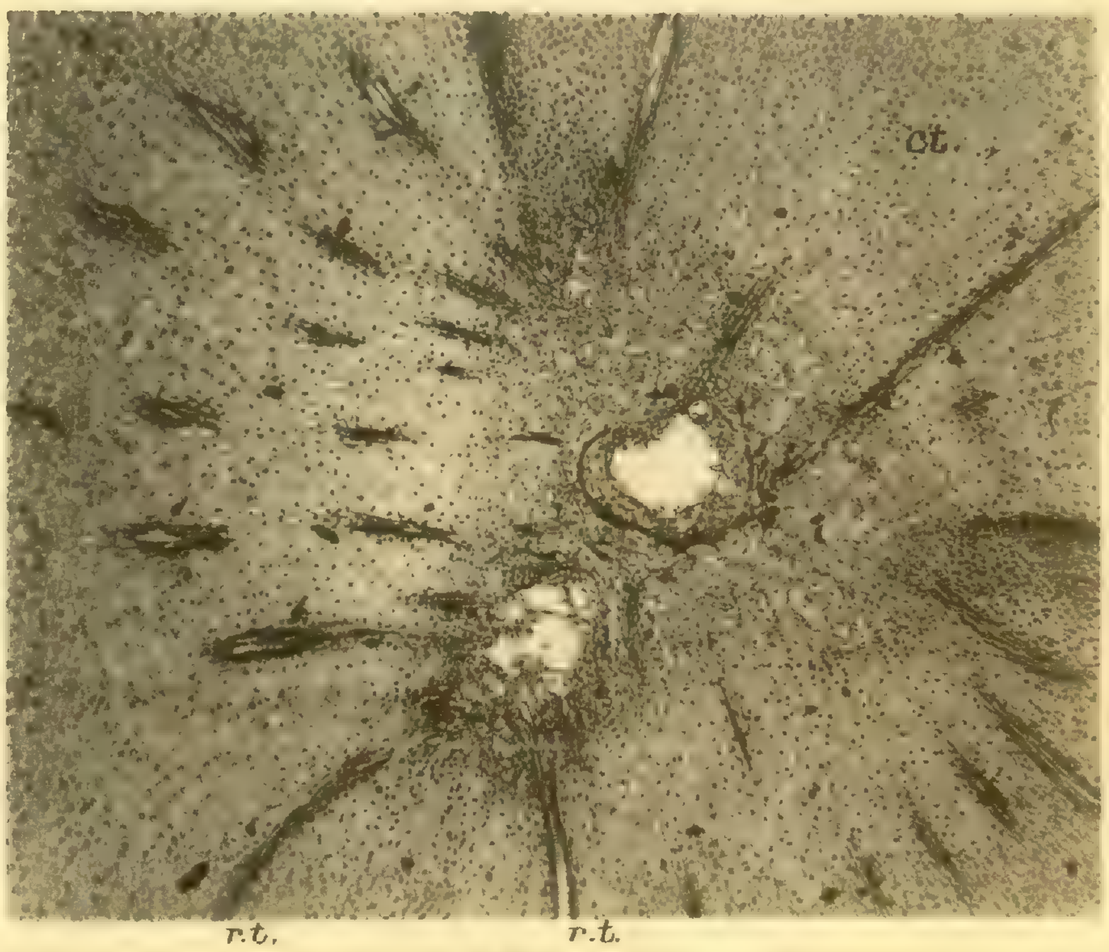
74.



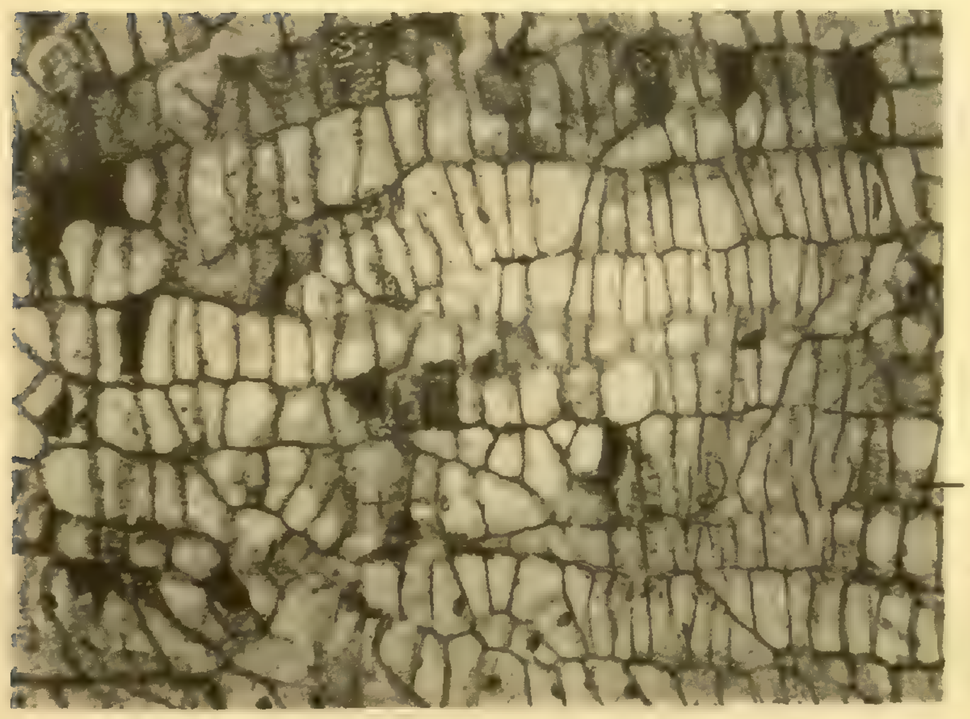
78.



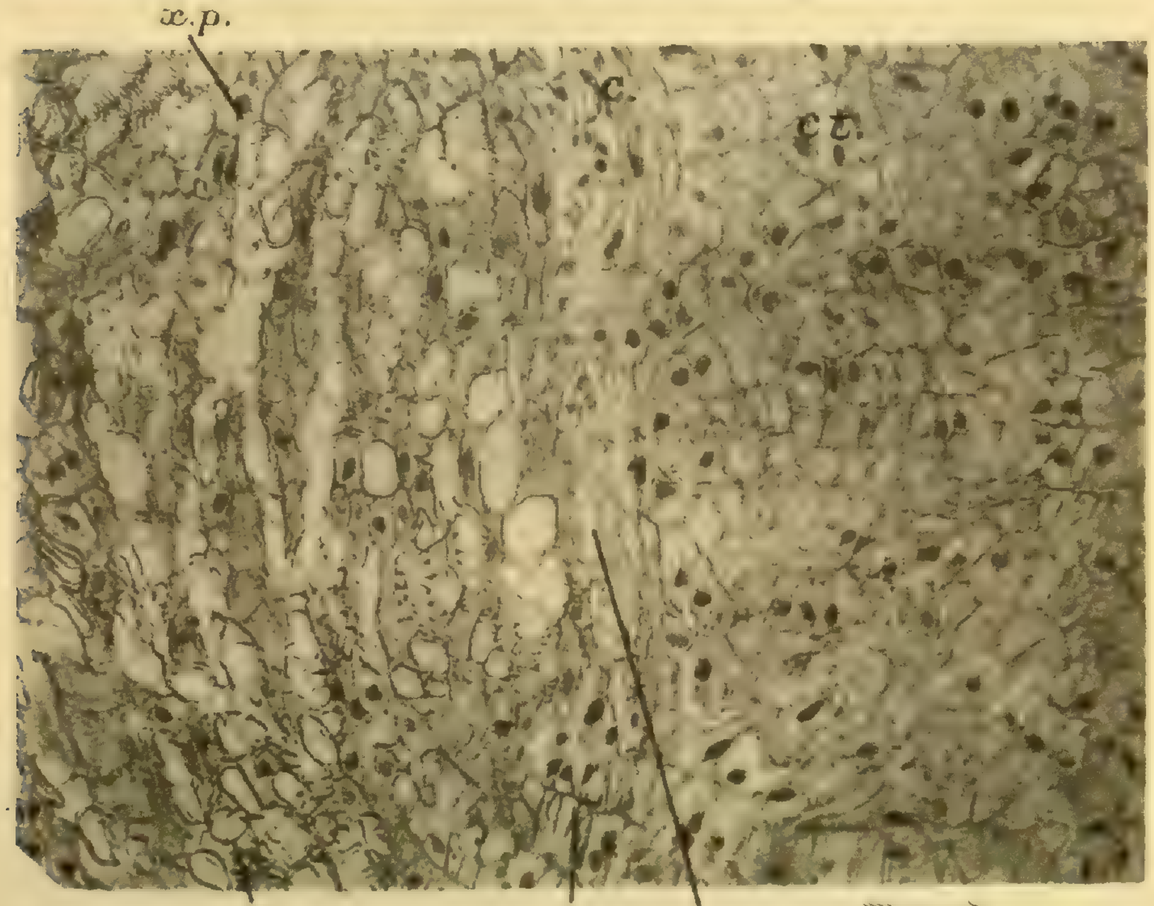
75.



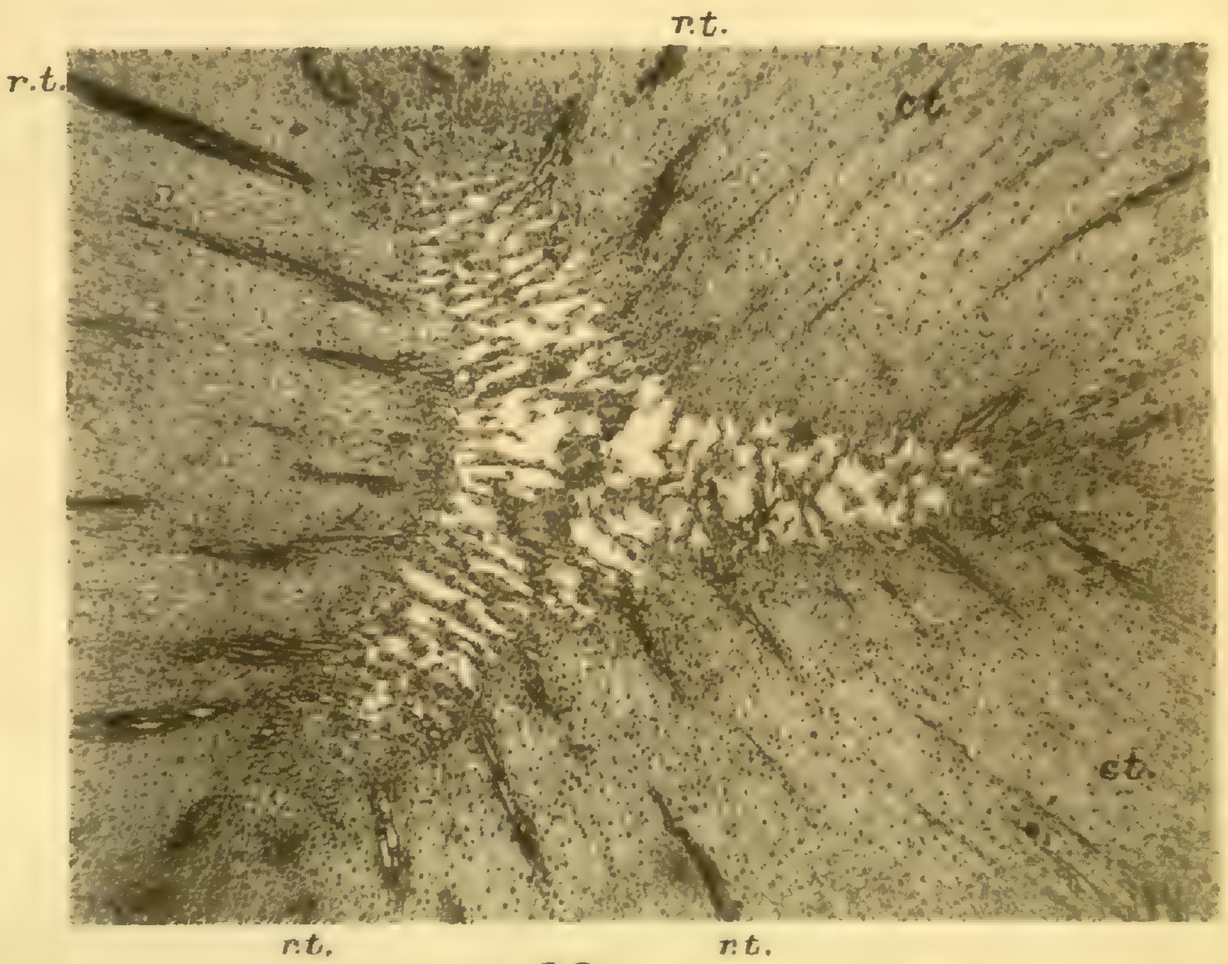
79.



76.



77.



80.

C.W. et H.T. phot

Huth coll

ISOETES JAPONICA. A. Br.

LINNEAN SOCIETY OF LONDON.

MEMORANDA CONCERNING TRANSACTIONS.

The First Series of the Transactions, containing those Memoirs and Communications that have been published in the Transactions of the Society, may be purchased, either in single Numbers, or parts to complete sets, by Members at the original prices. The price of the Index to Vols. I.–XXX. is 2s. to the public, and 1s. to Members: to Vols. XXXI.–XL. 2s. to the public, and 1s. to Members.

The Second Series of the Transactions is divided into Zoological and Botanical sections. The price of the Botanical parts of Vols. I.–V. to the public, and to Members, is the same as that of the Zoological parts (see wrapper).

Second Series.—Zoology.

Volume.	When Published.	Price to the Public.	Price to Members.
		£ s. d.	£ s. d.
I.	Parts I.–IX. (complete). 1875–80.	3 1 0	2 1 0
II.	Parts I.–XVI. (complete). 1881–87.	6 16 10	5 2 3
III.	Parts I.–XI. (complete). 1883–94.	7 12 10	5 14 8
IV.	Parts I.–IV. (complete).		
V.	Part I. 1885.	0 9 0	0 6 9
	Part II. 1885.	0 12 6	0 9 0
	Part III. 1886.	0 8 6	0 4 6
	Part IV. 1886.	1 6 0	0 15 0
	Part V. 1886.	0 14 0	0 10 6
	Part VI. 1886.	0 4 6	0 3 0
	Part VII. 1887.	0 4 6	0 3 0
	Part VIII. 1887.	0 6 0	0 4 6
	Part IX. 1888.	0 12 6	0 9 0
	Part X. 1888.	0 8 6	0 6 0
	Part XI. 1888.	0 7 0	0 5 3
	Part XII. 1889.	0 12 6	0 9 0
	Part XIII. 1890.	0 1 6	0 1 2
	Part XIV. 1890.	0 3 6	0 2 3
	Part XV. 1890.	0 6 6	0 4 6
VI.	Part I. 1891.	1 16 0	1 2 6
	Part II. 1891.	0 6 6	0 4 6
	Part III. 1892.	0 15 0	0 12 6
	Part IV. 1892.	0 8 6	0 6 0
	Part V. 1893.	0 8 0	0 6 0
	Part VI. 1893.	0 12 6	0 9 0
	Part VII. 1894.	0 12 0	0 9 0
	Part VIII. 1894.	0 12 6	0 9 0
	Part IX. 1894.	0 7 0	0 5 3
	Part X. 1894.	0 14 0	0 10 6
	Part XI. 1895.	0 6 0	0 4 6

Second Series.—Botany.

Volume.	When Published.	Price to the Public.	Price to Members.
		£ s. d.	£ s. d.
VII.	Part I. 1894.	0 5 0	0 3 9
	Part II. 1895.	0 5 0	0 4 6
	Part III. 1895.	0 3 0	0 2 3
	Part IV. 1895.	0 7 0	0 5 3
	Part V. 1895.	0 10 0	0 7 6
	Part VI. 1897.	0 4 6	0 3 0
	Part VII. 1897.	0 6 0	0 4 6
	Part VIII. 1897.	0 5 0	0 3 9
	Part IX. 1898.	0 3 0	0 2 3
	Part X. 1898.	0 7 0	0 5 3
	Part XI. 1898.	0 4 0	0 3 0
	Part XII. 1899.	0 12 0	0 9 0
	Part XIII. 1900.	0 5 0	0 3 9
	Part XIV. 1900.	0 6 0	0 4 6
	Part XV. 1901.	0 6 0	0 4 6
	Part XVI. 1902.	0 3 0	0 2 3
	Part XVII. 1902.	0 8 0	0 6 0
	Part XVIII. 1902.	0 5 0	0 3 9
	Part XIX. 1902.	0 3 0	0 2 3
	Part XX. Index.	0 2 0	0 1 6
VIII.	Part I. 1903.	1 0 0	0 15 0
	Part II. 1903.	0 8 0	0 6 0
	Part III. 1903.	0 8 0	0 6 0
	Part IV. 1903.	0 4 0	0 3 0
	Part V. 1903.	0 10 0	0 7 6
	Part VI. 1904.	0 12 0	0 9 0
	Part VII. 1904.	0 12 0	0 9 0
	Part VIII. 1905.	0 15 0	0 11 3

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

TITLEPAGE, CONTENTS, AND INDEX.

LONDON:

PRINTED FOR THE LINNEAN SOCIETY

BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

SOLD AT THE SOCIETY'S APARTMENTS, BURLINGTON HOUSE, PICCADILLY, W.1.

AND BY LONGMANS, GREEN, AND CO., PATERNOSTER ROW, E.C.4.

September 1922.

BOTANICAL
RECEIVED

INDEX.

[Note.—Synonyms and Native Names are printed in *italics*. A star * is added to names which appear to be used for the first time; a † for fossils.]

Abelia, *R. Br.*, mentioned, 251; vascular tissue, 252, 253, 260.
Acanthopanax, *Decne. & Planch.*, mentioned, 248, 259, 260.
Acanthophora, *Lamx.*, 123.
orientalis, *J. Ag.*, 107, 123; mentioned, 109.
specifera, *Börges.*, mentioned, 123.
Thierii, Lamx., mentioned, 123.
Adoxa, *Linn.*, mentioned, 240, 295.
Alangiaceæ, mentioned, 241, 242, 243, 268.
Alangieæ, mentioned, 267, 268.
Alangium, *Linn.*, 265–268; mentioned, 242, 289, 291, 296.
Alsinoideæ, mentioned, 295.
Altingia, *Nor.*, mentioned, 295.
Amentiferæ, mentioned, 241, 243.
Amphibiæ (*Isoëtes*), mentioned, 366, 367, 368.
Amphiroa, *Lamx.*, 141.
foliacea, *Lamx.*, 107, 141; mentioned, 110.
fragilissima, *Lamx.*, 107, 141; mentioned, 110.
Amphisbetema *, *Weber-van Bosse*, 133; mentioned, 106; ftnote, 135.
indica *, *Weber-van Bosse*, 108; mentioned, 110, 133, 134, 135, 136.
Anacardium, *Rottb.*, mentioned, 152.
Angiosperms, mentioned, 300, 301, 313, 316, 318, 323, 324, 325, 327, 328, 329, 369.
Anomozamites Nilssoni *† (*Phill.*), *Sew.*, n. comb., 187–188; mentioned, 189, 190, 195, 196, 198, 199.
Anomozamites Wiellandiella *†, *Sew.*, mentioned, 188.
Antithamnion, *Naegeli*, 136.
adnatum, *J. Ag.*, 107, 136; mentioned, 110.
Aporosa, *Blume*, mentioned, 278.
Aquaticæ, mentioned, 366, 367, 368, 369.
Aquifoliaceæ, mentioned, 299.
Aralia, *Linn.*, mentioned, 244, 248, 256, 259, 260, 273, 280, 289, 290, 293, 296, 299, 300.
Araliaceæ, mentioned, 240, 241, 242, 244, 259, 273, 278, 280, 281, 296, 299.
Aralieæ, mentioned, 242.
Araucarian stems, mentioned, 94.
Araucarieæ, mentioned, 95, 96, 97, 99, 100.
Araucarineæ, mentioned, 71.
Arber, A., An Anatomical Study of the Palæozoic Cone-genus *Lepidostrobus*, 205–232.
Arthrotaxites indicus †, *Oldh. & Morris*, mentioned, 71.
Aucuba, *Linn.*, 269–273; mentioned, 241, 242, 244, 261, 271, 277, 286, 287, 290, 291, 293, 296, 297, 298.
himalaica, *Hook. f. & Thoms.*, mentioned, 269, 270, 289.
japonica, *Linn.*, mentioned, 269, 270, 289, 298.
Aucubeæ, mentioned, 272.
Avrainvillea amadelpha, *A. & E. Gepp*, mentioned, 106.
Balanophora, *Forst.*, mentioned, 145, 146, 147.
Balanophoraceæ, 143; mentioned, 146.
Bancroft, N., On some Indian Jurassic Gymnosperms, 69–81.
—— *Rhexoxylon africanum*, A new Medullosean Stem, 87–101.
Bennetittalean frouds, mentioned, 99.
—— group, mentioned, 196.
Bennettitales †, 179–189; mentioned, 198, 199.
Bennettites Gibsonianus †, *Carruth.*, mentioned, 76.
Morierei †, *Lign.*, 182, 183; mentioned, 197.
Benstedtia †, *Sew.*, mentioned, 72.
Benstedti †, *Knowlton*, 73.
Benthamia, *Lindl.*, mentioned, 242, 261, 264.
Betula, *Linn.*, mentioned, 268, 277, 278.
Betulaceæ, mentioned, 295.
Bignonia spp., mentioned, 345.
Bowenia, *Hook.*, mentioned, 157, 160, 171, 172, 173, 174, 177, 181, 183, 197.
serrulata, Chamberlain, 172.
spectabilis, *Hook.*, var. serrulata, *André*, 172, 173; mentioned, 175, 176.
Brachyoxylon notabile †, *Holl. & Jeffr.*, mentioned, 72.
Brachyphyllum †, *Brongn.*, 71.
macrocarpum †, *Newberry*, mentioned, 71.
mamillare †, *Brongn.*, 71–72.
Brugmansia, *Pers.*, mentioned, 147.
Bruniaceæ, mentioned, 296.
Bucklandia, *R. Br.*, mentioned, 247.

Bucklandia Milleriana †, *Carruth.*, mentioned, 69.
Bucklandioideæ, mentioned, 246, 247.
Buxus balearica, *Lam.*, mentioned, 296.

Cactaceæ, mentioned, 298.
Calamus Rotang, *Linn.*, mentioned, 345.
Calliblepharis, *Kütz.*, 117.
prolifera, *J. Ag.*, 106, 117; mentioned, 106.
Campanulaceæ, mentioned, 297.
Camptotheca, *Decne.*, mentioned, 242.
Caprifoliaceæ, 251–260; morphology of ovary, 251–255; ovule, 255–256; vascular tissue, 256–258; summary, 258–260; mentioned, 240, 243, 245, 264, 273, 281, 287, 294, 295, 301.
Carboniferous Pteridosperms, mentioned, 156.
Carpinus Betulus, *Linn.*, mentioned, 250.
Castanea, *Linn.*, mentioned, 243, 244, 268, 297.
Casuarinaceæ, mentioned, 299.
Ceramiaceæ, 135; mentioned, 110.
Ceramium, *Lyngb.*, 136.
cinnabarinum, *Hauck*, 107; mentioned, 110, 136.
sp., 107, 108, 137; mentioned, 110.
Cerasus juliana, *hort.*, mentioned, 298.
Ceratophyllaceæ, mentioned, 299.
Ceratophyllum, *Linn.*, mentioned, ftnote 344.
Ceratozamia, *Brongn.*, 157, 166, 167; mentioned, 174, 175, 177.
fusco-viridis, *D. Moore*, 166, 167.
Küsteriana, *Regel*, mentioned, 166, 167.
latifolia, *Miq.*, 166, 167.
mexicana, *Brongn.*, 166, 167; mentioned, 176.
Chætangiaceæ, 112; mentioned, 108.
Champia, *Desvaux*, 119.
compressa, *Harv.*, 107, 119; mentioned, 109, 120.
parvula, *J. Ag.*, 120.
Champia sp., 107, 119–120; mentioned, 109.
Chantransia, *Schmitz*, 111.
barbadensis, *Vickers*, mentioned, 111.
efflorescens, *Kjellm.*, mentioned, 111.
Liagoræ *, *Weber-van Bosse*, n.sp., 107, 111; mentioned, 108.
Nemalionis, *Vickers*, mentioned, 111.
Chlorophyceæ, mentioned, 105.
Chondria, *C. Agardh*, 125.
pumila, *Vick.*, 107, 125; mentioned, 109.
pusilla, *Hook.*, mentioned, 106.
simpliciuscula *, *Weber-van Bosse*, 125; mentioned, 107, 108, 110.
Chylocladia, *Grev.*, 120.
perpusilla *, *Weber-van Bosse*, 120; mentioned, 108, 109.
Cladhymenia, *Hook. & Harv.*, 124.
oblongifolia, *Hook. & Harv.*, 108, 124; mentioned, 106, 109.
Cladoxyleæ, mentioned, 98, 99.
Cladoxylon †, *Unger*, mentioned, 98.
Kidstoni †, *Solms*, mentioned, 98, 99, 101.
Cochlospermaceæ, mentioned, 299.
Codium, *Ag.*, mentioned, 132.
Cœlarthrum, *Börges.*, 120.
Albertisii, *Börges.*, 107, 120–121; mentioned, 109.
Cœlochondria, *Falk.*, mentioned, 125.
Colpoxylon †, *Brongn.*, mentioned, 96, 98.
œduense †, *Brongn.*, mentioned, 98.
Combretaceæ, mentioned, 242, 267, 268, 296, 297.
Compositæ, 294; mentioned, 297.
Coniferæ, mentioned, 71, 73.
Coniferocaulon †, *Fliche*, 72.
Benstedtii †, *Stopes*, 73.
colymbeæforme †, *Sew.*, 72.
sp. †, 72, 73; internal structure, 85–86.
Conifers, mentioned, 199.
Corallinaceæ, 141; mentioned, 110.
Corallopsis, *Grev.*, 117.
Cacalia, *J. Ag.*, 107, 117; mentioned, 109.
minor, *J. Ag.*, mentioned, 117.
Cordaiteæ †, mentioned, 95, 96, 97, 99, 100.
Cordaitean stems, mentioned, 94.
Cornaceæ, 261–291; mentioned, 239, 240, 242, 243, 244, 245, 248.
Corneæ, mentioned, 241, 242, 261, 264.
Cornoideæ, mentioned, 239.
Cornus, *Linn.*, 261–265; mentioned, 241, 242, 248, 268, 272, 273, 276, 277, 281, 283, 290, 291, 295, 296.
alba, *Linn.*, mentioned, 261, 262, 265.
Amomum, *Mill.*, mentioned, 261.
mas, *Linn.*, mentioned, 261, 262.
sanguinea, *Linn.*, mentioned. 261, 262, 263.
Corokia, *A. Cunn.*, mentioned, 242, 244, 261, 282, 283, 286, 287, 290, 291, 296, 299.
Cotoneaster, *Raoul*, mentioned, 282, 290.
Corylaceæ, mentioned, 299.
Corylopsis, *Sieb. & Zucc.*, mentioned, 245, 248, 250, 251, 299.
spicata, *Sieb. & Zucc.*, vascular tissue, 249; mentioned, 247, 248, 249.
Corylus Avellana, *Linn.*, mentioned, 300.
Cratægus Oxyacantha, *Linn.*, mentioned, 298.
Cruoriella, *Crouan*, mentioned, 138.
Cruoriopsis, *Dufour*, 140.
cruciata, *Dufour*, 108, 140–141; mentioned, 110.
Cryptomeria japonica, *D. Don*, mentioned, 329.
Cryptonemia, *J. Ag.*, 138.
seminervis, *J. Ag.*, 108, 138; mentioned, 110.
sp., 108, 138; mentioned, 110.
Ctenis †, *Lindl. & Hutt.*, mentioned, 190, 196, 199.
falcata †, *Lindl. & Hutt.*, 193–194; mentioned, 190.
sp. †, mentioned, 178.
Ctenozamites †, *Nath.*, mentioned, 178.
Cupressineæ, mentioned, 71, 72.
Curtisia, *Ait.*, mentioned, 241, 242.
Cycadaceæ, mentioned, 100, 161.
Cycadales, mentioned, 196, 199.

Cycadean cuticles, mentioned, 157, 191.
fronds, mentioned, 74, 156, 188, 197, 199.
stems, mentioned, 188.
Cycadeoidea †, *Buckl.*, mentioned, 76, 78.
gigantea †, *Sew.*, mentioned, 78.
ingens †, *Ward*, mentioned, 75, 80.
Cycadeoideæ, mentioned, 78.
Cycadeoidean rhachis, mentioned, 75.
Cycadophyta, mentioned, 79, 156, 195.
Cycadopteris Brauniana †, Zeill., 178.
Cycads, mentioned, 75, 78, 80, 155–200, 313.
Cycas, *Linn.*, 160–162; mentioned, 90, 157, 174, 198.
circinalis, *Linn.*, 160, 161; mentioned, 162, 173, 177.
media, *R. Br.*, 160.
Micholitzii, *Dyer*, 160, 161.
revoluta, *Thunb.*, 160, 161; mentioned, 162, 175, 177, 191.
undulata, *Desf.*, 160, 161.

Dasya, *Ag.*, mentioned, 135.
elegans, *Ag.*, mentioned, 128.
indica, *J. Ag.*, 105; mentioned, 106.
Dasyeæ, mentioned, 128.
Dasyopsis, *Zanard.*, 128; mentioned, 127.
aperta *, *Weber-van Bosse*, 128–129; mentioned, 110, 126, 127.
cervicornis, *Falkenb.*, mentioned, 129.
Geppii *, *Weber-van Bosse*, 130; mentioned, 107, 108, 110, 126, 131.
palmatifida *, *Weber-van Bosse*, 130–131; mentioned, 107, 108, 110.
spinella, *Zanard.*, mentioned, 129.
Stanleyi *, *Weber-van Bosse*, 108, 128; mentioned, 110, 129, 130.

Davidia, *Baill.*, 239, 240; mentioned, 242, 243, 244, 248, 267, 273, 280, 288, 289, 290, 291, 292, 293, 296, 299.
involucrata, *Baill.*, mentioned, 239, 298.
Delesseria hypoglossoides, *Harv.*, 121.
Delesseriaceæ, 121; mentioned, 109.
Dermonema, *Grev.*, 112.
dichotomum, *Harv.*, 107, 112; mentioned, 108.
Dicoryphe, *Thou.*, mentioned, 248.
Dicotyledons, sterility in, mentioned, 294.
Dictyopteris falcata †, Morris, mentioned, 74.
Dictyozamites †, *Oldh.*, 74–76; mentioned, 178, 185, 189, 196.
falcatus †, *Oldh.*, nob., 74, 75, 76; mentioned, 80.
Hawelli †, *Sew.*, 186; mentioned, 178.
indicus †, *Feist.*, mentioned, 74.
Johnstrupi †, *Nath.*, mentioned, 178, 186, 187.
Dictyurus, *Bory*, 135.
purpurascens, *Bory*, 107, 108, 135; mentioned, 110.
Diervilla, *Linn.*, mentioned, 256, 260, 295, 301.
Lonicera, *Mill.*, floral structure, 254; mentioned, 255.
Dilleniaceæ, mentioned, 299.
Dioon, *Lindl.*, 157, 165; mentioned, 166, 174, 175, 177, 191, 198.
angustifolium, *Miq.*, mentioned, 175.
edule, *Lindl.*, 165, 166; mentioned, 175, 177.
spinulosum, *Dyer*, 165, 166.
Dioonites Buchianus †, *Ettingsh.*, 195.
Dunkerianus †, *Schenk*, 178, 195.
Dipelta, *Maxim.*, mentioned, 253.
Disanthus, *Maxim.*, mentioned, 251.
cercidifolia, *Maxim.*, mentioned, 247.
Distylium, *Sieb. & Zucc.*, 245–247; mentioned, 250, 296.
Dracæna Benstedtii †, *König*, mentioned, 72.

Echinostrobus expansus †, Feistm., 71.

Elodea, *Michx.*, mentioned, 363; ftnote, 344.
Empetraceæ, mentioned, 299.
Encephalartos, *Lehm.*, 162–164; mentioned, 157, 174, 177, 197, 198.
Altensteinii, *Lehm.*, 174.
caffer, *Miq.*, 162; mentioned, 164; ftnote, 166.
Ghellinckii, *Lem.*, 162, 164; mentioned, 177.
horridus, *Lehm.*, 162, 163.
lanuginosus, *Lehm.*, 162.
Laurentianus, *Wilden.*, 162.
Lehmanni, *Eckl.*, 162, 163, 164.
villosus, *Lemaire*, 162, 163, 164.
Woodii, *hort.*, 162, 163.
Endosiphonia, *Zanard.*, mentioned, 106, 123, 124, 134.
clavigera, *Falkenb.*, mentioned, 124.
Ephedra, *Linn.*, mentioned, 313, 314, 316, 317, 318, 322, 323, 325, 326, 327.
campylopoda, *DC.*, 313, 314.
distachya, *Forsk.*, mentioned, ftnote 328.
Equisetales, mentioned, 370.
Ethelia *, *Weber-van Bosse*, n. subgen., 138; mentioned, 140.
Eucheuma, *J. Ag.*, 115.
Cottonii *, *Weber-van Bosse*, 108, 115; mentioned, 109.
Schrammi, *Crouan*, mentioned, 115.
spinosum, *J. Ag.*, mentioned, 115.
Eu-Isoëtes * (§), *C. West & Takeda*, 369, 371.
Eupeyssonnelia *, *Weber-van Bosse*, n. subgen., 139.
Euphorbia virgata, *Waldst. & Kit.*, mentioned, 329.
Euryomma, *Schmitz*, mentioned, 115.
Eustigma, *Gardn. & Champ.*, mentioned, 246, 250.

Fagaceæ, mentioned, 299.
Fauchea, *Mont. & Bory*, 118.
microspora, *Born.*, 108, 118; mentioned, 109.
Filicales, mentioned, 369, 370.
Flora of Frankonia, mentioned, 178.

Forstiera, A. S. Horne, error for Forestiera, *Poir.*, mentioned, 278.
Fothergilla, *Murr.*, mentioned, 248, 250, 251.
Gardeni, *Murr.*, 248; vascular tissue of, 249.
major, *Lodd.*, vascular tissue of, 249; mentioned, 247, 248, 249, 250.
Frenelopsis Hoheneggeri †, *Schenk*, mentioned, 178.
Fucus obtusus, Huds., 121.
Valentiæ, Turn., 118.

Galaxaura, *Lamx.*, 112.
collabens, *J. Ag.*, mentioned, 113.
fastigiata, *Decne.*, 107, 108, 113; mentioned, 108.
hawaiiana, *Butt.*, 108, 113; mentioned, 108.
Liebmanni, *Kjellm.*, 107, 112, 113; mentioned, 108.
obtusata, *Lamx.*, 108, 113; mentioned, 108.
veprecula, *Kjellm.*, 107, 113; mentioned, 108.
Garrya, *Dougl.*, 274–278; mentioned, 241, 242, 261, 272, 273, 280, 290, 291, 296, 301.
elliptica, *Dougl.*, mentioned, 241, 245, 274, 275, 277, 290; vascular tissue, 276.
Fadyenii, *Hook.*, mentioned, 274, 275, 277, 290.
Fremontii, *Torr.*, mentioned, 275.
gracilis, *Wang.*, mentioned, 275.
laurifolia, *Benth.*, mentioned, 274, 275, 277.
longifolia, *Rose*, mentioned, 276.
Macfaydiana, Carrière, sphalm., 275.
ovata, *Benth.*, mentioned, 274.
Thuretii ×, *Carrière*, mentioned, 241, 275, 276, 289.
Veatchii, *Kellogg* (err. Veitchii), mentioned, 275, 276.
Wrightii, *Torr.*, mentioned, 274, 275.
Garryaceæ, mentioned, 241, 242, 243, 277.
Garryales, mentioned, 277.
Gates, R. R., A Contribution to a Knowledge of the Mutating Œnotheras, 1–62.
Gelidiaceæ, mentioned, 109, 114.
Gelidiopsis, *Schmitz*, 116; mentioned, 137.
rigida, *Weber-van Bosse*, 107, 116; mentioned, 109.
variabilis, *Schmitz*, 107, 116; mentioned, 109, 119, 126.
Gelidium, *Lamx.*, 114; mentioned, 137.
crinale, *Lamx.*, 107, 114; mentioned, 109.
pannosum, *Grun.*, 107, 114; mentioned, 109.
rigidum, Okamura, 116.
Gelinaria, *Sond.*, mentioned, 137.
Geranium longipes, *DC.*, mentioned, 297.
Gigartinaceæ, 114; mentioned, 109.
Ginkgo, *Linn.*, mentioned, 199.
Ginkgoales, mentioned, 179.
Gloioderma, *J. Ag.*, 119.
expansa*, *Weber-van Bosse*, 108, 119; mentioned, 108.
Gloiophlœa, *J. Ag.*, 112.
articulata*, *Weber-van Bosse*, 108, 112; mentioned, 108.
scinaioides, *J. Ag.*, mentioned, 112.
Gloiothamnion Schmitzianum, Rheinbold, 137.
Gnetales, mentioned, 199, 316.
Gnetoideæ, mentioned, 328.
Gnetum, *Linn.*, mentioned, 175, 325, 326, 327, 329.
africanum, *Welw.*, 311; macrospore and endosperm, 318–322; described, 323; mentioned, 312, 317, 327.
Brunonianum, Griff., 312.
Bucholzianum, *Engl.*, mentioned, 312, 314.
campylopoda, lapsu = Ephedra campylopoda, 313.
edule, *Blume*, mentioned, 319.
Gnemon, *Linn.*, 311–318; male flower microspore and pollen-grain, 316–318; mentioned, 119, 319, 320, 321, 322, 327.
Leyboldi, *Tul.*, mentioned, 312, 313.
moluccanum, *Lotsy*, mentioned, 318.
ovalifolium, *Poir.*, mentioned, 319.
Rumphianum, *Becc.*, mentioned, 319.
scandens, *Roxb.*, mentioned, 316.
Gnetum Ula, *Brongn.*, mentioned, 319.
Gracilaria, *Grev.*, 116; mentioned, 115.
compressa, *Grev.*, 107, 116, 117; mentioned, 109.
Grateloupiaceæ, 137; mentioned, 110.
Griffithsia, *Ag.*, 135.
sp., 108, 135; mentioned, 110.
Griselinia, *Forst. f.*, 284–287, 299; mentioned, 242, 261, 290, 291, 293, 296.
littoralis, *Raoul*, vascular tissue, 285; mentioned, 245, 284, 286, 290.
lucida, *Forst. f.*, vascular tissue, 285; mentioned, 245, 284, 285, 286, 287, 291.
Gunnera, *Linn.*, mentioned, ftnote 329.
Gymnosperms, mentioned, 156, 157, 175, 179, 197, 199, 200, 313, 325, 327, 328, 330.

Haloplegma, *Mont.*, 136.
Preissii, *Sond.*, 108, 136; mentioned, 110.
Halymenia, *J. Ag.*, 137.
Durvillæi, *Bory*, mentioned, 137.
formosa, *Harv.*, mentioned, 137.
polyclada *var.* aldabradensis*, *A. & E. Gepp*, 108, 137; mentioned, 110.
Hamamelidaceæ, 240–251; mentioned, 259, 260, 264, 265, 273, 277, 278, 293, 295, 296, 297, 299.
Hamamelis, *Gronov.*, mentioned, 240, 245, 247, 248, 250, 251, 264, 273, 277, 296, 299.
arborea, *Ottol.*, vascular tissue, 249; mentioned, 247, 248, 249.
chinensis, *R. Br.*, mentioned, 246.
virginica, *Linn.*, mentioned, 247, 248.
Zuccariniana, *Ottol.*, vascular tissue, 249; mentioned, 247, 250.
Harvey-Gibson, R. J., Observations on the Morphology and Anatomy of the Genus *Mystropetalon*, Harv., 143–153.
Hedera, *Linn.*, mentioned, 259, 260, 296.
Helix, *Linn.*, mentioned, 292.

Helminthocladiaceæ, 111; mentioned, 108.
Helwingia, *Willd.*, 278–283; mentioned, 241, 242, 261, 273, 290, 291, 293, 295, 296, 298.
ruscifolia, *Willd.*, mentioned, 279, 298.
Helwingiaceæ, mentioned, 241, 242, 267, 277.
Herposiphonia, *Naegeli*, 126; mentioned, 136.
prorepens, *Schmitz*, 107, 126; mentioned, 110.
Heterosiphonia, *Mont.*, 132; mentioned, 135.
Rendlei *, *Weber-van Bosse*, 108, 132, 137; mentioned, 110, 137.
sp., 107, 108, 132; mentioned, 110.
subsecundata, *Falk.*, mentioned, 132.
Horne, A. S., A Contribution to the Study of the Evolution of the Flower, with special reference to the Hamamelidaceæ, Caprifoliaceæ, and Cornaceæ, 239–306.
Hydrangea, *Gronov.*, mentioned, 295.
Hyoscyamus virginianus, Alpino, 16, 17, 18.
Hypnea, *Lamx.*, 117.
divaricata, *Grev.*, 108, 117; mentioned, 109.
pannosa, *J. Ag.*, 107, 108, 118, 125; mentioned, 109, 125.
spathulata, *J. Ag.*, mentioned, 121.
sp., 107, 118; mentioned, 109.
Valentiæ, *Mont.*, 107, 118; mentioned, 109, 117.
Hypoglossum, *Kütz.*, 121.
sp., 107, 121; mentioned, 109.

Ilex Pernyii, *Franch.* (err. Perneyi), mentioned, 296.
Inula, *Linn.*, mentioned, 244, 290, 299.
Iridæa, *Bory*, 114.
sp., 106, 108, 114; mentioned, 109.
Isoëtes, *Linn.*, mentioned, 333, 334, 336, 337, 340, 343, 344, 345, 346, 351, 352, 357, 360, 361, 366, 368, 370, 371.
Isoëtes Butleri, *Engelm.*, mentioned, 368.
Durieui, *Bory*, mentioned, 337, 343, 345.
echinospora, *Durieu*, mentioned, 345, 356, 363, 364, 368.
—— *var.* Braunii, mentioned, 368.
Engelmanni, *A. Br.*, mentioned, 345, 363.
Hystrix, *Bory*, mentioned, 338, 343, 345, 346, 361, 364.
japonica, *A. Br.*, 333–372; stem, 340–346; rhizophore, 346–351; roots, 351–358; leaves, 358–365; bud-protection, 365.
lacustris, *Linn.*, mentioned, 336, 337, 338, 340, 341, 343, 345, 346, 348, 356, 357, 359, 362, 364, 365, 371.
melanopoda, *J. Gay*, mentioned, 345, 368.
Nuttalli, *A. Br.*, mentioned, 345.
saccharata, *Engelm.*, mentioned, 368.
setacea, *Bosc*, mentioned, 358.
tegulensis, *Genn.*, mentioned, 368.
Tuckermanii, *A. Br.*, mentioned, 368.
velata, *A. Br.*, mentioned, 337, 338, 343.

Jania, *Lamx.*, 141.
tenella, *Kütz.*, 107, 141; mentioned, 110.
Juglans, *Linn.*, mentioned, 277, 278.
regia, *Linn.*, mentioned, 297, 298, 300.

Kaliphora, *Hook. f.*, mentioned, 242.

Lathyrus odoratus, *Linn.*, mentioned, 292.
Laurencia, *Lamx.*, 121.
ceylanica, *J. Ag.*, 107, 108, 123; mentioned, 109.
indica, *Hauck*, mentioned, 122.
Laurencia nidifica, *J. Ag.*, 108, 121; mentioned, 109.
obtusa, *Lamx.*, 107, 108, 121–122; mentioned, 109.
—— *var.* racemosa, *Kütz.*, mentioned, 122.
pannosa, *Zanard.*, mentioned, 122.
papillosa, *Grev.*, var. australica, *Kütz.*, 107, 108, 120; mentioned, 109, 125.
pygmæa *, *Weber-van Bosse*, 107, 122; mentioned, 109.
spinulifera, *Kütz.*, 107, 122; mentioned, 109.
Lepidodendreæ, mentioned, 369.
Lepidodendron †, *Sternb.*, 207; mentioned, 370, 371.
Harcourtii †, Binney, 206.
vasculare †, Binney, 206.
Veltheimianus †, Sternb., 206, 207.
Lepidophloios †, *Sternb.*, mentioned, 224.
Lepidostrobus †, *Brongn.*, 205–232.
Bertrandi †, *Zalessky*, 207; mentioned, 215.
Binneyanus *†, *A. Arber*, 212–217; form of cone and sporophylls, structure of cone axis, 212, 213; sporophyll traces in axis, 213; structure of sporophyll, 213–214; ligule, 214; sporangium, 214–215; spores, 215; mentioned, 211.
brevifolium †, *Lesq.*, mentioned, 218.
Brownii †, *Schimp.*, 206; mentioned, 207, 211, 224, 231, 232.
foliaceus †, *Maslen*, 287, 208–211; mentioned, 216.
gracilis *†, *A. Arber*, 217–220; cone and sporophylls, 217–218; structure of cone axis, 218; sporophyll traces in axis, 218; sporophyll, 218–219; ligule, 219; sporangium, 219; spores, 219; mentioned, 211, 221.
laminatus †, *A. Arber*, mentioned, 210.
majus †, *Brongn.*, mentioned, ftnote 208.

Lepidostrobus oldhamius †, *Will.*, 208–211; sterile plate in sporangium, 208–211; periderm in the sporophylls, 211; mentioned, 206, 215, 223.
—— *f.* minor *†, *A. Arber*, 220–223; form of cone and sporophylls, 221; sporophyll traces in axis, 221; structure of sporophylls, 221–222; spores, 222.
—— *f.* pilosus *†, *A. Arber*, 223–232; form of cone and sporophylls, 224; structure of cone axis, 224–225; sporophyll traces in axis, 225; structure of sporophyll, 226–227; ligule, 227; sporangium, 228; spores, 228; mentioned, 211.
variabilis †, *Lindl. & Hutt.*, 208.
Veltheimianus †, *Scott*, 206; mentioned, 207, 209, 211.
Wünschianus †, *Binney*, 206, 207.
Leycesteria, *Wall.*, mentioned, 243, 251, 253, 255, 256, 258, 259, 260, 273, 296, 297, 299.
formosa, *Wall.*, vascular tissue, 272; mentioned, 256.
Liagora, *Lamx.*, 111.
elongata, *Zanard.*, mentioned, 111.
hawaiiana, *Butt.*, 111, 112; mentioned, 108, 111.
orientalis, *J. Ag.*, 107, 111; mentioned, 108.
Lilium, *Linn.*, mentioned, 244, 278, 290, 299.
Linnæa, *Gronov.*, mentioned, 251, 253, 256, 260.
borealis, *Linn.*, vascular tissue, 252.
Liquidambar, *Linn.*, mentioned, 247, 251, 293, 295.
styraciflua, *Linn.*, mentioned, 247, 248.
Lithothamnia, *Fosl.*, mentioned, 105.
Loasaceæ, mentioned, 299.
Lomentaria, *Lyngbye*, mentioned, 120.
Albertisii, Picc., 120.
intertexta, Kütz, 120.
Lonicera, *Linn.*, mentioned, 241, 243, 251, 255, 256, 260, 293, 297.
Lonicera Caprifolium, *Linn.*, mentioned, 251.
Periclymenum, *Linn.*, vascular tissue, 252.
Lonicereæ, mentioned, 260.
Loropetalum, *R. Br.*, 250; mentioned, 240, 246, 296.
chinense, *Oliver*, mentioned, 246.
Lycopodiales, mentioned, 369, 370.
Lycopodineæ, mentioned, 269.
Lycopodium, *Linn.*, mentioned, 230, 340, 369.
Lycopods, mentioned, 337, 369, 370.
Lysimachia americana, Columna, 16, 17.
angustifolia, spicata lutea Lusitanica, Barrelier, 17.
corniculta minor lutea Canadensis, Morison, 17.
latifolia, spicata, lutea Lusitanica, Barrelier, 17.
lutea corniculata, Bauhin, 16, 17.
—— —— *latifolia Lusitanica*, Barrelier, 17.
—— —— *non papposa Virginiana major*, Morison, 17.
—— —— —— —— *minor*, Morison, 17.
—— *flore globoso*, Park., Ger., Morison, 17.
—— *siliquosa Virginiana*, Parkinson, 17.
—— *Virginiana*, Ray, 17.
Virginiana altera, foliis latioribus, floribus, luteis, majoribus, Ray, 17, 18.
—— *angustifolia corniculata*, Morison, 17.
—— *latifolia lutea corniculata*, Morison, 17.

Macrozamia, *Miq.*, 157, 167, 172, 174, 175, 197.
corallipes, *Hook.*, 167, 168; mentioned, 70.
cylindrica, *C. Moore*, 167, 168, 169, 170, 177.
Denisonnii, *F. Muell.*, 167, 168, 169.
Fraseri, Miq., 167, 168.
Hopei, *T. Hill*, 167, 168, 169.
Macleayi, Miq., 167, 168.
spiralis, *Miq.*, 167, 168, 170; mentioned, 177.
Marattiaceæ, mentioned, ftnote, 342.
Marlea, *Roxb.*, 265–268; mentioned, 241, 242, 244, 261, 277, 290, 297.
barbata, *R. Br.*, mentioned, 265.
begonifolia, *Roxb.*, mentioned, 265, 267, 291.
platanifolia, *Sieb. & Zucc.*, mentioned, 265, 266, 267, 272.
Mastixia, *Blume*, mentioned, 241.
Medullosa †, *Cotta*, mentioned, 89, 96, 97, 98, 100, 101.
anglica †, *Scott*, mentioned, 91, 97.
Leuckarti †, *Göpp. & Stenz.*, mentioned, 96, 97.
Ludwigii †, *Göpp. & Stenz.*, mentioned, 98.
porosa †, *Cotta*, mentioned, 90, 96, 97.
Solmsii †, *Schenk*, mentioned, 91, 96, 97, 98.
—— *var.* incrassata *†, *Bancr.*, mentioned, 96.
—— *var.* lignosa *†, *Bancr.*, mentioned, 96, 97.
—— *var.* typica *†, *Bancr.*, mentioned, 96.
stellata †, *Cotta*, mentioned, 90, 96, 97.
Medulloseæ, mentioned, 90, 94, 96, 98, 99, 100, 101.
Melanophylla, *Baker*, 284; mentioned, 242, 261, 287.
alnifolia, *Baker*, mentioned, 284.
aucubæifolia, *Baker*, mentioned, 284.
Humbloti, *Baill.* (non descr.), mentioned, 284.
Melanothamnus, *Born. & Falk.*, mentioned, 134, 135.
Melobesia, *Lamx.*, 141.
callithamniodes, *Falk.*, 107, 141; mentioned, 110.
Meryta, *Forst.*, mentioned, 280, 281.
Mesozoic Cycadean fronds, 178; Cycadophyta, 80; flora, mentioned, 80; fronds, mentioned, 156.
Microcycas, *A. DC.*, 157.
Monocotyledons, mentioned, 294.
Musa, *Linn.*, mentioned, 31.

Myeloxylon †, *Brongn.*, mentioned, 93.
Myrica, *Linn.*, mentioned, 277.
pensylvanica, *hort.*, mentioned, 300.
Myricales, mentioned, 277.
Myrtifloræ, mentioned, 268.
Mystropetalon, *Harv.*, 143–153; rhizome and its relation to host plant, 145–147; inflorescence, 147; male flower, 148–149; female flower, 149–151; fruit, 151–152; identification, 152–153.
Polemanni, *Harv.*, 143, 144, 145; mentioned, 149, 150, 151, 152; described, 153.
Sollyi *, *Harvey Gibson*, 153.
Thomii, *Harv.*, 143, 144, 145; mentioned, 148, 149, 150, 151, 152; described, 153.
Myxophyceæ, mentioned, 105.

Nilssonia†, *Brongn.*, 190; mentioned, 178, 179.
brevis †, *Brongn.*, mentioned, 190.
compta †, *Bronn*, 190–191; mentioned, 192, 193, 196.
mediana †, *Fox-Strangw.*, 191–192; mentioned, 190, 191, 192, 196.
orientalis †, *Heer*, 192–193; mentioned, 191, 196.
polymorpha †, *Schenk*, mentioned, 178, 190, 192.
pterophylloides †, *Nath.*, mentioned, 190, 196.
sp., 192.
tenuinervis †, Nath., 192, 193.
Nilssoniales, 190–196.
Nilssoniopteris †, Nath., 192; mentioned, 193.
Nitophyllum, *Grev.*, 121.
sp., 107, 108, 121; mentioned, 109.
Nyssa, *Gronov.*, 287–291; mentioned, 241, 242, 243, 244, 261, 280, 290, 291, 296, 299.
capitata, *Walk.*, mentioned, 264.
sessiliflora, *Hook. f. & Thoms.* mentioned, 281.
sylvatica, *Marsh.*, 287, 288, 299.
Nyssaceæ, mentioned, 241, 242, 243, 268, 289.

Ochnaceæ, mentioned, 299.
Œnothera, *Linn.*, 1–62; mentioned, 292, 293, 294.
albida, *De Vries*, mentioned, 37, 44.
ammophila, *Focke*, 11; mentioned, 42.
argillicola, *MacK.*, 11, 12, 13.
biennis, *Linn.*, 11, 12, 39–40; mentioned, 3, 4, ftnote 13, 14, 15, 16, 17, 18, 19, 20, 21, 27, 28, 41, 42, 43, 44, 45, 46, 47, 48, 51, 52, 53, 54, 55, 56, 57, 59, 60, 61.
—— × O. gigas, mentioned, 51.
—— × O. lævifolia, mentioned, 53, 56.
—— × —— —— læta, mentioned, 56.
—— × O. Lamarckiana, mentioned, 53, 55, 56.
—— × —— —— læta, mentioned, 56.
—— × —— —— velutina, mentioned, 56.
—— × —— ——, velutina × O. Lamarckiana, mentioned, 56.
—— × O. muricata, mentioned, 55.
—— × O. nanella, mentioned, 54, 56.
—— × O. rubricalyx, mentioned, 56.
—— [*var.*] grandiflora, mentioned. 47.
blanda, *Schout.*, mentioned, 30.
brevistylis, *De Vries*, 4, 27–28; mentioned, 16, 21, 22, 23, 40, 47, 51, 55, 61.
canovirens, *Steele*, 11, 13; mentioned, 14, 39.
cheradophila, *Bartlett*, 11, 13; mentioned, 14.
cognata, *Hort. Panorm.*, mentioned, 11, 33, 34, 30.
Drummondii, *Hook.*, 11, 12, 13.
elliptica, *De Vries*, mentioned, 45.
erythrosepala, Barb., 47.
Œnothera *foliis lanceolatis, dentatis, caule hispido*, Miller, 17.
—— *ovato-lanceolatis planis*, Miller, 17.
fruticosa, *Linn.*, mentioned, 17.
gigas, *De Vries*, 2, 4, 5, 6, 31–34; mentioned, 34, 35, 46, 49, 50, 51, 52, 55, 58, 59, 60, 61, 292.
—— × O. biennis, mentioned, 51.
—— × O. brevistylis, mentioned, 51.
—— × O. Lamarckiana, mentioned, 51.
—— × O. muricata, mentioned, 51.
—— × O. rubrinervis, mentioned, 51.
—— [*var.*] nanella, mentioned, 32, 33, 34.
grandiflora, *Solander*, 11, 12, 38–39; mentioned, ftnote 13, 14, 15, 16, 17, 18, 19, 20, 24, 25, 27, 35, 40, 42, 44, 45, 46, 47, 59, 60, 61.
Heribaudi, *Lévl.*, 11, 13; mentioned, 14.
Hookeri, *Torr. & Gray*, 11, 12; mentioned, 14, 19, 20, 27.
Jamesii, *Torr. & Gray*, 11, 12, 13.
læta, *De Vries*, mentioned, 28, 52, 53, 54, 55, 56, 57, 61.
lævifolia, *De Vries*, 4, 26–27; mentioned, 21, 22, 23, 29, 30, 32, 33, 37, 53.
—— [*var.*] nanella, *Schout.* (?), mentioned, 27.
—— [*var.*] salicifolia, *De Vries*, mentioned, 27.
Lamarckiana, *Ser.*, variations and mutations, 20–26; mentioned, 2–61, 67.
—— × O. biennis, mentioned, 53, 54, 55, 56.
—— × —— —— × (O. biennis × O. Lamarckiana), mentioned, 57.
—— × —— × O. Lamarckiana, mentioned, 55, 56.
—— × O. brevistylis, mentioned, 35.
—— × O. gigas, mentioned, 49, 50, 51.
—— × O. rubricalyx, mentioned, 49, 50.

Œnothera Lamarckiana × O. rubrinervis, mentioned, 49.
Lamarckiana, *Ser.*, *var.* cruciata, mentioned, 11, 25.
lata, *De Vries*, 5, 35–38, 293; mentioned, 21, 26, 28, 32, 35, 37, 44, 45, 47, 48, 49, 50, 51, 52.
—— × O. gigas, mentioned, 51, 52.
—— × O. Lamarckiana, mentioned, 35, 37, 48, 49, 50.
—— × O. nanella, mentioned, 50.
—— × O. rubrinervis, mentioned, 49.
—— × O. semilata, mentioned, 37.
—— nanella (?), mentioned, 34, 37, 38.
MacBrideæ, *Nels.*, 11, 12, 13.
macrosceles, *A. Gray*, 11, 12, 13.
muricata, *Linn.*, 40–42; mentioned, 2, 3, 11, 14, 15, 16, 17, 18, 19, 20, 27, 28, 41, 43, 55, 57, 60.
—— × O. biennis, mentioned, 55.
—— × O. gigas, mentioned, 51.
—— *var.* canescens, *Robinson*, 11, 13; mentioned, 41, 42, 43.
mut. albida, *De Vries*, mentioned, 11.
—— brevistylis, *De Vries*, mentioned, 11.
—— elliptica, *De Vries*, mentioned, 11.
—— fatua, *De Vries*, mentioned, 11.
—— gigas, *De Vries*, mentioned, 11.
—— lævifolia, *De Vries*, mentioned, 11.
—— —— nanella, mentioned, 11.
—— —— salicifolia, mentioned, 11.
—— lata, *De Vries*, mentioned, 11.
—— leptocarpa, *De Vries*, mentioned, 11.
—— nanella, *De Vries*, mentioned, 11.
—— —— elliptica, mentioned, 11.
Œnothera *mut.* nanella lata, mentioned, 11.
—— —— oblonga, mentioned, 11.
—— —— scintillans, mentioned, 11.
—— oblonga, *De Vries*, mentioned, 11.
—— rubrinervis, *De Vries*, mentioned, 11.
—— scintillans, *De Vries*, mentioned, 11.
—— semilata, *De Vries*, mentioned, 11.
—— spathulata, *De Vries*, mentioned, 11.
—— sublinearis, *De Vries*, mentioned, 11.
—— subovata, *De Vries*, mentioned, 11.
nanella, *De Vries*, 5, 34–35; mentioned, 21, 24, 32, 33, 37, 38, 46, 48, 50, 53, 54, 56, 58, 59.
—— -albida, mentioned, 34.
—— × O. biennis, mentioned, 53, 54, 56.
—— × —— —— × (O. Lamarckiana × O. biennis), mentioned, 56.
—— -elliptica, mentioned, 34, 38.
—— -oblonga, mentioned, 34, 38.
—— [*var.*] rubrinervis, mentioned, 50.
—— [*var.*] scintillans, mentioned, 34, 38.
Oakesiana, *Robbins*, 11, 12; mentioned, 14.
oblonga, *De Vries*, mentioned, 37, 44, 49, 56.
ornata, *Nels.*, 11, 12; mentioned, 14, 19, 40.
parviflora, *Linn.*, 11; mentioned, 14.
pusillus *, *Gates*, 107; mentioned, 110.
rhombipetala, *Nutt.*, 11, 13; mentioned, 14.
rubricalyx, *Gates*, 5, 6, 11, 28–31; mentioned, 21, 26, 28, 29, 49, 53, 55, 56, 57, 58, 61.
—— × O. biennis, mentioned, 56.
—— × O. Lamarckiana, mentioned, 49.
—— × O. nanella, mentioned, 49.
Œnothera rubrinervis, *De Vries*, 6, 28–31; mentioned, 11, 19, 23, 24, 26, 27, 28, 29, 35, 41, 44, 47, 49, 50, 51, 53, 57, 58, 61.
—— × O. gigas, mentioned, 51.
—— × O. Lamarckiana, mentioned, 29, 30, 35, 49, 57.
—— × —— —— × O. Lamarckiana × O. rubrinervis), mentioned, 57.
—— × O. nanella, mentioned, 35, 49, 50.
—— nanella, mentioned, 50.
scintillans, *De Vries*, mentioned, 27, 293.
—— *nanella*, 11.
semilata, *De Vries*, 35–38.
Simsiana, *Ser.*, 11, 12, 13; mentioned, 16, 40.
sinuata, *Linn.*, mentioned, 14.
strigosa, *MacK. & Bush*, 11, 13; mentioned, 14, 39.
suaveolens, Desf., 47.
Tracyi, *Bartlett*, 11, 12; mentioned, 14, 40.
velutina, *De Vries*, mentioned, 28, 52, 53, 54, 55, 56, 57, 61.
Oleaceæ, mentioned, 278.
Oleandra, *Cav.*, mentioned, 188.
Oleandridium *, *Schimp.*, mentioned, 188.
Oligocladus, *Weber-van Bosse*, 126; mentioned, 106.
Boldinghii, *Weber-van Bosse*, mentioned, 126, 127.
Prainii *, *Weber-van Bosse*, 107, 126–127; mentioned, 110.
pusillus *, *Weber-van Bosse*, 127.
Onagra angustifolia caule rubro, flore minori, Tourn., 17.
angustifolia, Tourn., 17.
latifolia, Tourn., 17.
—— *floribus amplis*, Tourn., 17.
Ophioglossaceæ, mentioned, ftnote, 342.
Osmunda, *Linn.*, mentioned, 344.
Otopteris †, Lindl. & Hutt., mentioned, 178.
Otozamites †, *Braun*, mentioned, 75, 178, 179, 187, 188, 195, 196, 197, 198.
acuminatus †, *Schenk*, mentioned, 178.
Beani †, *Sew.*, mentioned, 178.
Bucklandi †, *Schenk*, 178.

Otozamites Feistmanteli †, *Zigno*, 186.
graphicus †, *Leck.*, 178, 186, 188.

Paramecium, *Duj.*, mentioned, 29.
Parrotia, *C. A. Mey.*, mentioned, 245, 248, 250, 251.
Jacquemontiana, *Decne.*, vascular tissue, 249; mentioned, 247, 248, 249.
Paulownia imperialis, *Sieb. & Zucc.*, 227; mentioned, 226.
Pearson, H. H. W., Notes on the Morphology of certain Structures concerned in Reproduction in the Genus *Gnetum*, 311–330.
Penea, Pearson, err.=Penæa, *Linn.*, mentioned, ftnote 329.
Peperomia, *Ruiz & Pav.*, mentioned, 328; ftnote, 329.
Peyssonnelia, *Decne.*, 139; mentioned, 138.
biradiata *, *Weber-van Bosse*, 140; mentioned, 107, 110.
calcea, *Heydr.*, 107, 139; mentioned, 110.
coccinea, *J. Ag.*, 107, 108, 139; mentioned, 110.
conchicola, *Picc. & Gran.*, mentioned, 139.
Harveyana, *Crouan*, 108, 139; mentioned, 106, 110.
polymorpha, *Schmitz*, 108, 139–140.
—— *f.* Gardineri *, *Weber-van Bosse*, 108, 139–140; mentioned, 110.
Phæocordylis, *Griff.*, mentioned, 145.
Phæophyceæ, mentioned, 105.
Phyllantheæ, mentioned, 278.
Pisum sativum, *Linn.*, mentioned, 292.
Pleuromeia †, *Corda*, mentioned, 337, 369, 370.
Polycœlia, *J. Ag.*, 114.
van Hoevellii *, *Weber-van Bosse*, 114; mentioned, 107, 109.
Polyosma, *Blume*, mentioned, 260, 293, 295, 296, 301.
Polypetalæ, mentioned, 301.
Polysiphonia, *Grev.*, 125; mentioned, 127.
sp., 107, 125; mentioned, 110.
Potamogeton, *Linn.*, mentioned, ftnote 344, 363.
Primula, *Linn.*, mentioned, 51, 294.
floribunda *var.* isabellina × P. kewensis, mentioned, 51.
sinensis, *Sabine*, mentioned, 292, 293.
Prunus, *Linn.*, mentioned, 296.
Pseudendosiphonia, *Weber-van Bosse*, 123; mentioned, 106, 108, 109.
Gardineri *, *Weber-van Bosse*, 123–124.
Pseudocycas †, *Nath.*, mentioned, 178, 179, 194, 195.
Psilotaceæ, mentioned, ftnote, 342.
Psilotales, mentioned, 370.
Pteridosperms, mentioned, 98, 199.
Pterophyllum †, *Brongn.*, mentioned, 178, 179, 195.
spp., mentioned, 178.
Ptilophyllum †, *Morris*, 73–74, 75, 76, 180, 182, 195, 196, 198, 199; mentioned, 75; fronds, mentioned, 184.
acutifolium †, *Oldh. & Morris*, 73; mentioned, 75.
cutchense †, *Feistm.*, 73; mentioned, 70, 74, 75, 79.
hirsutum †, *H. H. Thomas*, mentioned, ftnote 183.
pecten *†, *Morris*, n. comb., 179, 180, 181, 182, 183; mentioned, 185, 187, 189.
sp. †, 183, 184.
Ptilozamites †, *Nath.*, mentioned, 178, 179, 190, 196, 198, 199.
Leckenbyi †, *Nath.*, 194; mentioned, 190.
Pyrus, *Linn.*, mentioned, 296.
Malus, *Linn.*, mentioned, 298.

Quercus, *Linn.*, mentioned, 243, 244, 268.
Robur, *Linn.*, mentioned, 300.
Quisqualis, *Linn.*, mentioned, 293.

Rafflesia, *R. Br.*, mentioned, 147.
Ralfsia expansa, *J. Ag.*, mentioned, 138.
Ralfsiaceæ, mentioned, 140.
Ranunculaceæ, mentioned, 299.
Ranunculus fluitans, *Lam.*, mentioned, 360.
Reinboldiella, *De Toni*, 137.
Schmitziana, *De Toni*, 107, 137; mentioned, 110.
Rhexoxylon *†, *N. Bancr.*, 100.
africanum *, *N. Bancr.*, 87–101; affinities and reference of specimen, 96–100; external characters, 87–88; internal structure, 88–89; structure of ground-tissue, 89; structure of steles, 91–93.
Rhizantheæ, 143.
Rhizophoraceæ, mentioned, 268.
Rhodoglossum, *J. Ag.*, mentioned, 114.
Rhodoleia, *Champ.*, mentioned, 244, 246, 247, 250, 260.
Championi, *Hook.*, mentioned, 246.
Teysmanni, *Miq.*, mentioned, 246.
Rhodomelaceæ, 121; mentioned, 109, 110, 128, 135.
Rhodophyceæ, 105; mentioned, 106.
Rhodophyllidaceæ, 114; mentioned, 109.
Rhodophyllis peltata, *Grun.*, mentioned, 119.
Rhodymenia prolifera, Harv., 117.
Rhodymeniaceæ, 118; mentioned, 109, 119.
Ricinus communis, *Linn.*, mentioned, 300.
Rosaceæ, mentioned, 244, 248, 290, 295, 296, 298, 299.
Roschera, *Sond.*, 125.
africana, Sond., 126.
glomerulata *, *Weber-van Bosse*, 125; mentioned, 107, 110.

Salicaceæ, mentioned, 295.
Salicales, mentioned, 277.
Salix, *Linn.*, mentioned, 277, 278.
Sambucaceæ, 240, 260, 264, 265.
Sambucus, *Linn.*, mentioned, 240, 243, 244, 253, 255, 256, 258, 259, 264, 265, 273, 291, 292, 295, 296.
canadensis, *Linn.*, mentioned, 264, 265.
nigra, *Linn.*, floral structure, 254; mentioned, 265.
Santalaceæ, mentioned, 289.
Sapindaceæ, mentioned, 296, 297.
Sarconema, *Zanard.*, 114.
furcellatum, *Zanard.*, 107, 114, 115; mentioned, 109.
Saxifraga, *Linn.*, mentioned, 250, 251.

Saxifragaceæ, mentioned, 260, 264, 295, 298, 299.
Saxifragineæ, mentioned, 246, 248.
Scepa, Lindl., 278.
Scinaia, *Bivona*, mentioned, 112.
Scolopendrium, *Sm.*, mentioned, 188.
Scrophulariaceæ, mentioned, 226.
'Sealark' Expedition, mentioned, 106.
Selaginella, *Spring*, mentioned, 369, 370.
lævigata, *Baker, var.* Lyallii, *Spring*, mentioned, 232.
spinosa, *Beauv.*, mentioned, 337.
'Siboga' Expedition, mentioned, 105.
Sigillaria †, *Brongn.*, mentioned, 370.
Sigillarieæ, mentioned, 369.
"Sokolowa," type of nucleus, 327.
Sphærococcaceæ, 116; mentioned, 109.
Sphenolepidium †, *Heer*, mentioned, 71.
Sphenophyllales, mentioned, 369, 370.
Spiræa, *Linn.*, mentioned, 296, 299.
Ulmaria, *Linn.*, mentioned, 361.
Spyridia, *Harv.*, 136.
filamentosa, *Harv.*, 108, 136; mentioned, 110.
Squamariaceæ, 138; mentioned, 110.
Stangeria, *T. Moore*, 157, 158–160, 173; mentioned, 162, 171, 174, 175, 177, 181, 188, 197, 198.
paradoxa, *T. Moore*, mentioned, 158, 159, 198.
—— *var.* schizodon, mentioned, 158.
Stangerites †, *Bornem.*, mentioned, 188.
Steloxylon †, *Solms*, mentioned, 96, 98, 100, 101.
Ludwigii †, *Solms*, mentioned, 98.
Stereum purpureum, *Fr.*, mentioned, 364.
Stigmaria †, *Brongn.*, mentioned, 370.
Stragularia, *Stromf.*, 140.
Strebloclaclia, *Schmitz*, mentioned, 135.
Sutcliffia †, *Scott*, mentioned, 89, 96, 99.
insignis †, *Scott*, mentioned, ftnote 88, 98.
Sycopsis, *Oliver*, mentioned, 240, 246, 250, 296.
Sympetalæ, mentioned, 297, 299, 301.
Symphoricarpus, *Juss.*, mentioned, 253, 255, 256, 258, 259, 260, 293.
racemosus, *Michx.*, mentioned, 252, 253.

Tæniopteris †, *Brongn.*, 188, 195, 196, 198.
major †, *Lindl. & Hutt.*, 189; mentioned, 190.
stenoneura †, Schenk, 178.
vittata †, *Brongn.*, 188, 189; mentioned, 190, 192, 193.
Tapeinodasya, *Weber-van Bosse*, 131; mentioned, 106.
Bornetii, *Weber-van Bosse*, mentioned, 131, 132.
Ethelæ *, *Weber-van Bosse*, 131–132; mentioned, 110.
Taxus, *Linn.*, mentioned, 325, 326, 327.
Tetrathyrium subcordatum, *Benth.*, mentioned, 248.
Thinnfeldia †, *Ettingsh.*, mentioned, 178, 195.
spp. †, mentioned, 178.
Thomas, H. Hamshaw, and Nellie Bancroft, On the Cuticles of some Recent and Fossil Cycadean Fronds, 155–201.
Thuïtes expansus †, Phill., 71.
Todea, *Willd.*, mentioned, 344.
Tolypiocladia glomerulata, Schmitz, 125; mentioned, 126.
Trichocladus, *Pers.*, mentioned, 245, 250.
Triosteum, *Linn.*, mentioned, 260.
Triuridales, mentioned, 299.
Trophophyte of *Gnetum*, 323.

Udotea, *Lamx.*, mentioned, 120, 140.
Umbelliferæ, mentioned, 242.
Umbellifloræ, mentioned, 299.

Valerianaceæ, mentioned, 297.
Viburnum, *Linn.*, mentioned, 241, 243, 253, 256, 258, 259, 260, 272, 273, 286, 296, 297, 299.
Lantana, *Linn.*, floral structure, 254; mentioned, 253, 255, 257.
Viburnum Tinus, *Linn.*, mentioned, 255.
Völkelia †, *Solms*, mentioned, 98.

Weber-van Bosse, A., Marine Algæ, Rhodophyceæ, of the 'Sealark Expedition, collected by Mr. J. Stanley Gardiner (communicated by Gardiner), 105–141.
Welwitschia, *Hook. f.*, mentioned, 175, 199, 313–329.
West, Cyril, and H. Takeda, On *Isoëtes japonica*, A. Br., 333–372.
Wielandiella †, *Nath.*, mentioned, 188, 196.
angustifolia †, *Nath.*, 187.
Wikstroemia, *Endl.*, mentioned, 31.
Williamsonia †, *Carruth.*, mentioned, 69, 76, 180, 183, 184.
gigas †, *Carruth.*, mentioned, 70, 76, 180.
pecten †, *Carruth.*, mentioned, 79, 179, 180.
scotica †, *Sew.*, mentioned, 184.
Williamsonian type, fructification, 76; mentioned, 78, 80, 196; stems, 77, 78, 79.
Wilsonæa indica, *De Toni*, 133.

Yatesia †, *Carruth.*, mentioned, 69.

Zamia, *Linn.*, 157, 170; mentioned, 72, 75, 80, 159, 172, 174, 175, 177, 182, 197.
cylindrica, *Liebm.*, 170.
Fischeri, *Miq.*, 170, 171; mentioned, 172.
gigas †, *Lindl. & Hutt.*, mentioned, 180.
integrifolia, *Ait.*, 170, 172; mentioned, 173, 177.
Leiboldii, Miq., 170.
Lindeni, Regel, 170, 171, 172, 177.
Loddigesii, *Miq.*, 170; mentioned, 72.
muricata, *Willd.*, 170, 172.
—— *var.* picta, 174.
Ottonis, *Miq.*, 170, 171, 172.
Skinneri, *Warsz.*, 170, 171, 172; mentioned, 72, 85.
Zamites †, *Brongn.*, mentioned, 186, 195, 196, 197.
gigas †, *Lindl. & Hutt.*, 184, 185.
—— sp. †, 185.

PRINTED BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

LINNEAN SOCIETY OF LONDON.

MEMORANDA CONCERNING TRANSACTIONS.

The First Series of the Transactions, containing both Botanical and Zoological contributions, has been completed in 30 Vols., and a few entire sets are still for sale. Only certain single volumes, or parts to complete sets, may be obtained at the original prices. The price of the Index to Vols. 1–25 is 8*s.* to the public, and 6*s.* to Fellows; to Vols. 26–30, 4*s.* to the public, and 3*s.* to Fellows.

The Second Series of the Transactions is divided into Zoological and Botanical sections. The prices of the Botanical parts of these which have been published are as undermentioned. (For the Zoological parts see Zoological wrapper.)

SECOND SERIES.—BOTANY.

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
I. Parts I.–IX. (complete).	1875–80.	8	1	0	6	1	0
II. Parts I.–XVI. (complete).	1881–88.	6	16	10	5	2	3
III. Parts I.–XI. (complete).	1888–94.	7	12	10	5	14	8
IV. Parts I.–IV. (complete).	1894–95.	5	13	4	4	5	0
V. Part I.	1895.	0	9	0	0	6	9
Part II.	1895.	0	12	0	0	9	0
Part III.	1896.	0	6	0	0	4	6
Part IV.	1896.	1	0	0	0	15	0
Part V.	1896.	0	14	0	0	10	6
Part VI.	1896.	0	4	0	0	3	0
Part VII.	1897.	0	4	0	0	3	0
Part VIII.	1897.	0	6	0	0	4	6
Part IX.	1899.	0	12	0	0	9	0
Part X.	1899.	0	6	0	0	4	6
Part XI.	1899.	0	7	0	0	5	3
Part XII.	1899.	0	12	0	0	9	0
Part XIII.	1900.	0	1	6	0	1	2
Part XIV.	1900.	0	3	0	0	2	3
Part XV.	1901.	0	6	0	0	4	6
VI. Part I.	1901.	1	10	0	1	2	6
Part II.	1901.	0	6	0	0	4	6
Part III.	1902.	0	18	0	0	13	6
Part IV.	1903.	0	8	0	0	6	0
Part V.	1903.	0	8	0	0	6	0
Part VI.	1903.	0	12	0	0	9	0
Part VII.	1904.	0	12	0	0	9	0
Part VIII.	1904.	0	12	0	0	9	0
Part IX.	1904.	0	7	0	0	5	3
Part X.	1904.	0	14	0	0	10	6
Part XI.	1905.	0	4	0	0	3	0

SECOND SERIES.—BOTANY (*continued*).

Volume.	When Published.	Price to the Public. £	s.	d.	Price to Fellows. £	s.	d.
VII. Part I.	1904.	0	5	0	0	3	9
Part II.	1905.	0	6	0	0	4	6
Part III.	1906.	0	3	0	0	2	3
Part IV.	1906.	0	7	0	0	5	3
Part V.	1907.	0	10	0	0	7	6
Part VI.	1907.	0	4	0	0	3	0
Part VII.	1907.	0	6	0	0	4	6
Part VIII.	1908.	0	5	0	0	3	9
Part IX.	1908.	0	2	6	0	2	0
Part X.	1908.	0	7	0	0	5	3
Part XI.	1909.	0	4	0	0	3	0
Part XII.	1909.	0	12	0	0	9	0
Part XIII.	1909.	0	5	0	0	3	9
Part XIV.	1909.	0	6	0	0	4	6
Part XV.	1910.	0	6	0	0	4	6
Part XVI.	1912.	0	3	0	0	2	3
Part XVII.	1912.	0	8	0	0	6	0
Part XVIII.	1912.	0	5	0	0	3	9
Part XIX.	1912.	0	3	0	0	2	3
Part XX.	Index.	0	3	0	0	2	3
VIII. Part I.	1913.	1	0	0	0	15	0
Part II.	1913.	0	8	0	0	6	0
Part III.	1913.	0	8	0	0	6	0
Part IV.	1913.	0	4	0	0	3	0
Part V.	1913.	0	10	0	0	7	6
Part VI.	1914.	0	12	0	0	9	0
Part VII.	1914.	0	12	0	0	9	0
Part VIII.	1915.	0	18	0	0	13	6
Part IX.	1922. (Index)	4	0	0	0	3	0
IX. Part I.	1916.	1	18	0	1	8	6
Part II.	1922. (Index)	5	0	0	0	3	9